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ARTHUR HARMOUNT GRAVES
Brooklyn Botanic Garden
Brooklyn, New York

Notes on the Volvocales—I–IV

GILBERT MORGAN SMITH

(WITH PLATES 17, 18)

I. A CONSIDERATION OF THE SPECIES OF EUDORINA

A study of the various descriptions of *Eudorina elegans* Ehr. shows that a number of forms have been included under this collective name. Most authors describe the colony as spherical to subspherical in shape and as having a gelatinous envelope that is perfectly smooth in outline. Certain investigators [including Carter (1858), Chodat (1902), Conrad (1913), and Hartmann (1921)] have described colonies which are ellipsoid or ovoid in shape and with gelatinous envelopes that are distinctly mammillate at one pole. Hartmann's work shows that these recorded differences in colony shape cannot be ascribed to variation from generation to generation, since he maintained cultures of *Eudorina* through 1300 asexual generations and found that the colony shape was quite constant when the alga was grown under uniform conditions of chemical environment. It is true that Hartmann (1924) finds that a transfer from Benecke's to Molisch's solution induces the formation of a flattened colony which he calls the '*Gonium*-form,' although the designation '*Platydorina*-form' would be a better descriptive term. New colonies produced after the transfer of flattened colonies to Benecke's solution are of the normal *Eudorina* type. The constancy of colony types is also shown by the work of Grove (1915), who found only the spherical type in Great Britain, although he made a special effort to find colonies with posterior mammillations.

There seems, therefore, to be abundant justification for the contention of G. S. West (1916) that 'it would appear probable that there are two distinct races of *Eudorina*.' If this contention is granted, are the algae that have been described as *E. elegans* to be grouped in one collective species without named varieties or forms, as in Pascher's handbook (1927); are they to be given varietal recognition; or are they to be grouped in two species or series of species?

It seems to the writer that the last-named alternative is best and that the two types of *Eudorina* are sufficiently distinct to warrant specific recognition. To judge from the descriptions of *E. elegans* given by Ehrenberg, the spherical type of colony was the one which he had under observation when he described the genus, and it is only proper that his specific

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name should be retained for the spherical type. Probably even this restricted conception of the specific limits of *E. elegans* comprises a number of varieties and forms. Some of these differences rest on size alone, and Pascher (1927) has noted strains in which the colonies are always quite small.

It is clear that adult colonies of the ellipsoid or ovoid type, which have posterior mammillations, are not all of the same type. Adult cells of the strain cultivated through 1300 generations by Hartmann (1921) were characterized by chloroplasts with several pyrenoids each. Hartmann also had a strain under observation in which the chloroplasts of mature cells contained but a single pyrenoid, but he was unable to keep it under cultivation for a sufficient length of time to convince himself that the occurrence of a single pyrenoid in the chloroplast is a constant morphological character. The type of *Eudorina* with posteriorly mammillate ovoid colonies studied by Conrad (1913) always had 5–9 pyrenoids in adult cells. On the other hand, Chodat (1902) figures and describes colonies of this shape in which there is but a single pyrenoid in the chloroplasts of adult cells. Colonies of the latter type were sent me in an almost pure stand from a collection made at Stockton, California, by E. E. Stanford. This culture remained alive for over two months and in the hundreds of adult colonies observed the presence of a single pyrenoid was a quite constant character. The colonies of this *Eudorina* had posterior lobes which were distinctly mammillate, a feature which was much more noticeable in young than in old colonies, since the increase in diameter of the colony tends to obliterate the mammillations. While this is not the place, and it would be a rather profitless discussion, to consider what are specific limits among the algae, it may be pointed out that the regular occurrence of a single pyrenoid, or more than one pyrenoid, has become a well-established character in distinguishing between species of *Chlamydomonas*, and the presence of two or of several pyrenoids has been used to differentiate between species of *Chlorogonium*. In view of this well-accepted precedent, it seems best to refer the mamillate types of colony in *Eudorina* to distinct species. The name *E. plusicocca* is proposed for the species in which the chloroplasts contain several pyrenoids, and the name *E. unicocca* for that in which there is but a single pyrenoid in each chloroplast.

Observations which I have made upon living material from the Okoboji district in Iowa amply confirm the statements of Goroschankin (1875) and of Goebel (1882) that the colonies of *E. elegans* are dioecious. In this species every cell of a male colony gives rise to an antheridial packet of cells, which swims as a unit to the female colony, and there dissociates into the individual male gametes which swim slowly about within the gelatinous

envelope of the female colony. The material of *E. unicocca* collected at Stockton, California, also produced gametes, and sufficient cases were observed to state with certainty that this species is also dioecious and that each cell of a male colony develops into an antheridial packet. These packets were observed swimming about, but fertilization in this species was not observed with certainty.

Carter (1858), who was the first to observe gametic union in *Eudorina*, figures an ellipsoid colony with posterior mammillations, and shows that the four anterior cells of the colony develop into antheridial packets, and that the remaining cells of the colony function as eggs. Although these observations have not been confirmed since they were first described, this monoecious type of colony is sufficiently distinct to warrant specific recognition, and the name *Eudorina Carteri* is proposed for the species. *E. Carteri* cannot be distinguished from *E. plusicocca*, except when fruiting. Unfortunately there is no information available concerning the monoecism or dioecism of what is here recognized as *E. plusicocca*. The presumption is that it is dioecious, but if it should prove to be monoecious no specific distinction can be made between *E. plusicocca* and *E. Carteri*.

Three other well-defined species have been placed in the genus *Eudorina*. One of these, *E. charkowiensis* (Korshikow) Pascher, as will be shown on a later page (p. 365), belongs in *Pandorina*, the genus to which it was first assigned.

Eudorina echidna Swirenko (1926) is sharply differentiated from other species of *Eudorina* by the conical processes covering the entire surface of the gelatinous envelope. Pascher (1927) holds that it is not beyond the realm of possibility that further study may show that the structure of the colonial envelope has been erroneously described. For the present we can only accept Swirenko's statement concerning its structure.

E. illinoisensis (Kofoid) Pascher is a species originally assigned to the genus *Pleodorina*. The genus *Pleodorina* Shaw (1894) is distinguished from *Eudorina* by the fact that certain cells of the colony are purely vegetative and others are reproductive. *P. californica* Shaw, the type species, has about half the cells vegetative and the other half reproductive. This species has been reported from a number of stations in the United States, from France (Chatton, 1911), and from Russia (Swirenko, 1926). I have found that reproductive cells in colonies collected from the plankton of Wisconsin lakes (Smith, 1920) are 2–2.5 times the diameter of the vegetative cells. Practically all algologists are of the opinion that *Pleodorina* as exemplified by *P. californica*, is a genus sharply distinguishable from *Eudorina*. Opinion is not so certain, however, concerning the other species, *P. illinoisensis* Kofoid. Colonies of this species are usually 32-celled and with

the four anterior cells vegetative and the remainder reproductive. However, this distinction is relative rather than absolute, since both Kofoid (1898) and Grove (1915, 1917) find that in occasional colonies the small anterior cells have not completely lost the capacity to divide. Because of this Pascher (1927) transfers the species to *Eudorina*. While these aberrant colonies do show that the generic distinctions between *Eudorina* and *Pleodorina* do not hold in all individuals of this species, it seems better to the writer to retain the species in *Pleodorina*.

The two remaining species assigned to the genus, *E. stagnale* Wolle and *E. Steinii* (Playfair) Printz, have been so incompletely described that they are best considered as *species inquirendae*.

The five species which it is proposed to recognize may be distinguished from one another as follows:

Surface of colonial envelope without processes
  Colony spherical to broadly ellipsoid, without posterior mammillations of colonial envelope ..... 1. *E. elegans*
  Colony ellipsoid to ovate-ellipsoid, with posterior portion of colonial envelope mammillate
    Chloroplast of adult cells with several pyrenoids
      Sexual reproduction monoecious ..... 4. *E. Carteri*
      Sexual reproduction presumably dioecious ..... 2. *E. plusicocca*
    Chloroplast of adult cells with one pyrenoid ..... 3. *E. unicocca*
Surface of colonial envelope covered with short conical gelatinous processes ..... 5. *E. echidna*

1. EUDORINA ELEGANS Ehrenberg (pl. 17, figs. 1, 2), Abhand. Akad. Wiss. Berlin **1831**: 78. *pl. 2, f. 10A–10D.* 1832.

Colonies spherical to broadly ellipsoid in shape, gelatinous envelope of colony with a smooth outline. Colonies 32- or 64-celled, and with the cells not arranged in definite tiers. Cells approximately spherical in shape and with a cup-shaped chloroplast occupying most of the protoplast. Chloroplast of adult cells with several (usually 5–10) pyrenoids that lie more or less equidistant from one another. Each cell with a single stigma, stigmata at one pole of the colony frequently larger than those at the other.

Sexual reproduction heterogamous, dioecious, all cells of a colony developing into antheridia or functioning as eggs.

Colonies up to 110×125μ, cells up to 22μ diam.

World-wide in distribution.

2. **Eudorina plusicocca** sp. nov.

E. elegans Conrad non Ehrenberg, Recueil Inst. Leo Errera **9**: 321–343. *f. 1–13.* 1913; Hartmann, Arch. Protistenk. **43**: 223–286. *f. 1–7+pl. 1, 2.* 1921.

Colonies always ellipsoid or ovate-ellipsoid, distinctly mammilate at the

posterior pole, and with a smooth outline at the anterior pole. Generally 32-celled and with the cells in five transverse zones; the anterior and posterior zones containing four cells each, the three median tiers with eight cells each. Cells of anterior tier sometimes slightly smaller than those of other tiers. Cells spherical to subpyriform in shape and with a fairly massive cup-shaped chloroplast. Chloroplast of adult cells with 5–9 pyrenoids. Anterior cells of colony with a large stigma, posterior cells with stigma very small or lacking.

Sexual reproduction unknown.

Colonies 55–170μ long, 45–140μ broad (Conrad). Cells of free-swimming colonies 12–25μ in diameter (Conrad).

Definitely known only from Belgium (Conrad), and from Germany (Hartmann).

3. **Eudorina unicocca** sp. nov. (pl. 17, figs. 3, 4)

Eudorina elegans Chodat non Ehrenberg. Matér. pour la flore crypt. Suisse 1[3]: 152. *f. 76.* 1902.

Colonies always ellipsoid or ovate-ellipsoid, distinctly mammillate at the posterior pole and with a smooth outline at the opposite pole. Generally 32-celled and with the cells in five transverse tiers as in *E. plusicocca*. Cells of the anterior tier often slightly smaller than those of other tiers. Cells spherical to subpyriform in shape; if subpyriform, with the flattened side towards the face of the colony. Chloroplast cup-shaped, fairly massive, with one pyrenoid in basal portion even in adult cells. Anterior cells of colony with large stigma, intermediate tiers with smaller stigmata, posterior tier with very small stigmata or stigmata wanting.

Sexual reproduction heterogamous, dioecious, all cells of a colony developing, respectively, into antheridia or into eggs.

Free-swimming colonies (of California material) with colonies 60–110μ long, 50–95μ broad. Cells 5.5–18μ in diameter.

Thus far definitely known only from California, and from Switzerland (Chodat).

4. **Eudorina Carteri** sp. nov. (pl. 17, fig. 5)

Eudorina elegans Carter non Ehrenberg. Ann. and Mag. Nat. Hist. III. 2: 236–247. *pl. 8, f. 1–8.* 1858.

Colonies ellipsoid, with the posterior end distinctly mammillate and the anterior end smooth in outline. 16- or 32-celled. Cells spherical in outline, containing several pyrenoids when mature.

Sexual reproduction heterogamous, monoecious; the four cells at the anterior pole of the colony each developing into an antheridial packet, the remaining cells of the colony functioning as eggs.

Known only from the original station in India.

5. EUDORINA ECHIDNA Swirenko, Arch. Protistenk. **55**: 192. *f. A.* 1926.

Colonies 16-celled, ellipsoid, the entire surface of the colonial envelope not smooth but raised into short, conical, obtusely pointed elevations. Cells spherical, with cup-shaped chloroplasts containing a single basal pyrenoid.

Sexual reproduction unknown.

Colonies 160–185μ long, cells up to 19–20μ in diameter, cilia about 40μ long. Conical projections of colonial envelope 8–10μ long.

Known only from Ukrania (Southern Russia).

II. THE PHYLOGENY OF THE HIGHER COLONIAL VOLVOCALES

The foregoing splitting into a number of species of what has usually been considered a single species seems to lead to a clearer conception of evolution in the higher colonial Volvocales, especially that of *Platydorina*, *Pleodorina*, and *Volvox*.

The remarkable volvocine alga named *Platydorina* by Kofoid (1899) has been variously treated by those trying to construct a phylogenetic picture of the colonial Volvocales. Chief among the reasons for this diversity of opinion is the lack of knowledge of sexual reproduction in the genus. On the basis of colony organization it has been placed as close to *Gonium*, and at a lower level than *Pandorina* (Cavers, 1913, p. 110; Conrad, 1913); at a lower level than *Pandorina*, but not in the same line of descent as *Gonium* (Oltmanns, 1922); and as an immediate derivative of *Eudorina* (Kofoid, 1899; G. S. West, 1916). Recognition of the specific nature of the mammillate type of colony found in *Eudorina unicocca* and *E. plusicocca* shows that it is but a short step from these colonies to flattened ones with posterior projections of the colonial envelope such as are found in *Platydorina*. That such a flattening of the *Eudorina* colony may take place is shown by Hartmann's (1924) experiments. Hartmann calls these flattened colonies '*Gonium*-like,' because the 16-celled colonies have the same four interior cells and twelve peripheral cells as are found in *Gonium*. He overlooks the fact that 16-celled colonies of *Platydorina* have been shown to have the same cellular arrangement (Kofoid, 1899; Smith, 1926). There is also a striking similarity in the structure of cells of *Platydorina caudata* Kofoid and those of *Eudorina unicocca*. Both have cells which are subpyriform in shape and which contain but a single pyrenoid at the base of their cup-shaped chloroplast. In view of these similarities in colony and cell structure, the view that *Platydorina* is a genus derived from *Eudorina* seems the most probable.

There is almost universal agreement that *Pleodorina*, as represented by *P. californica* Shaw, represents a step forward from *Eudorina*. Many hold that by an increase in the number of cells in the colony and a further re-

duction in the number of reproductive cells *Pleodorina* has evolved into *Volvox*. Crow (1918) has put forward the suggestion, to which Fritsch (see West and Fritsch, 1927) adheres, that the evolution of *Volvox* has not been along this line, but in a different phylogenetic series and one which begins with a unicellular form of the nature of *Sphaerella* (*Haematococcus*) and thence through colonial forms such as *Stephanosphaera*. He places *Volvox* in the Sphaerellaceae because the cytoplasmic connections between *Volvox* cells are thought to be comparable to the cytoplasmic outgrowths of the protoplast found in *Sphaerella*, and because the cell structure is thought to be more like that of *Sphaerella* than that of *Chlamydomonas*. As far as the cellular structure is concerned, Crow's argument is not particularly convincing, since certain *Volvox* species, as *V. aureus* Ehr., have cells that are much more like those of *Chlamydomonas* than those of *Sphaerella*. At the time when he put forward his proposal, he supposed that all of the coenobic Volvocales but *Volvox* were without cytoplasmic connections between the cells. The recent demonstration of cytoplasmic connections between the cells in *Gonium*, *Pandorina*, and *Eudorina* (Bock, 1926) invalidates this argument, and shows that the orthodox view on the phylogeny of *Volvox* is probably the correct one.

III. PANDORINA CHARKOWIENSIS KORSHIKOW

The organism described by Korshikow (1923) as *Pandorina charkowiensis* has been known only from the original description. It differs from all other species of *Pandorina* and *Eudorina* in having a cup-shaped chloroplast which is not smooth in outline but with longitudinal ribs towards the anterior end of the cell. This type of chloroplast is not unique among the Volvocales and is found in several species of *Chlamydomonas*, including *C. Steinii* Gorosch. and *C. Kleinii* Schmidle. According to Korshikow the cells are subspherical to biscuit-shaped and with the flattened side towards the exterior of the colony. He states that the cells are not in mutual contact with one another as they lie embedded within the colonial envelope. Pascher (1925) thinks that the separation of the cells one from another within the colonial envelope shows that the species belongs to *Eudorina* and not in the genus to which it was first assigned.

During the past three years this species has been collected several times in California and was quite abundant in a collection from a pool near Stockton, and in one from a pool near Monterey. Many of the colonies from the Stockton collection were similar to Korshikow's figure and had the subpyriform cells some distance from one another within the colonial envelope (pl. 18, fig. 6). The majority of the colonies in the Stockton material had the cells closely apposed to one another in a manner

wholly typical for *Pandorina* (fig. 7). This was true both of the 32-celled colonies, which predominated in the collection, and of the 16-celled colonies. This finding of colonies with cells arranged in a fashion typical for *Pandorina* shows that it is better to retain the species in the genus where it was first described than to transfer it to *Eudorina*. The material does, however, bring out the fact that the vegetative features distinguishing *Eudorina* from *Pandorina* are not so sharp as algologists have thought, and that certain species of *Pandorina* may have individuals whose colonial organization approaches closely to that of *Eudorina*. The real distinction between the two lies in the isogamy of *Pandorina* and the heterogamy of *Eudorina*. The question of the genus to which this species is to be assigned cannot, therefore, be finally settled until its sexual reproduction is known.

As far as the cell structure is concerned, the California material is quite like that described by Korshikow. There is the same difference in size of stigmata in cells at opposite poles of the colony, and the same presence of 3–6 pyrenoids in each chloroplast. The chloroplasts show the same radial striations when seen in polar view, but I have been unable to satisfy myself whether this is due to a longitudinal ribbing on the surface of the chloroplast or to the type of longitudinal incision figured for the chloroplast of *Chlamydomonas Kleinii* Schmidle by G. S. West (1904).

IV. GONIUM FORMOSUM PASCHER AND GONIUM SOCIALE (DUJ.) WARMING

Two types of *Gonium* have long been recognized by algologists; in one type the colony may be sixteen-, eight-, or four-celled; in the other it is always four-celled. It has been customary to consider all individuals of the first type as belonging to a single species, *G. pectorale* Müller, but Pascher (1927) has recently recognized that there are two species with sixteen-celled colonies; *G. pectorale* in which the cells are broadly ellipsoid to ovoid and fairly close to one another, and *G. formosum* Pascher in which the cells are pyriform in shape and some distance from one another in the colony. He has found *G. formosum* in Holstein, and he also states that the *Gonium* which I have figured from the plankton of Wisconsin lakes (Smith 1920), is this species. During the past three years, collections of 16-celled *Gonium* colonies made in California have been examined critically to see to which species they belong, and it has been found that *G. formosum* is of more widespread occurrence than *G. pectorale*. In view of the wide local distribution of the two it does not seem improbable that the same condition obtains throughout the United States and that the two are to be found wherever a careful search is made for them. The only difference between the two species is in the structure of the cells and their arrangement within the colony, since fruiting material collected from a gold fish farm near Los

Altos shows that sexual reproduction takes place in the same manner as has been described for *G. pectorale*.

As far as the constantly four-celled type of *Gonium* is concerned, the morphological differences thus far described do not warrant the recognition of more than one species, *G. sociale* (Duj.) Warming. This species has been collected locally several times and once in great abundance from an outdoor gold fish pool at the home of Prof. J. I. W. Mac Murphy. In this particular collection there were thousands of four-celled colonies and not a single eight- or sixteen-celled one. The individual cells were ovoid in shape and with the posterior end somewhat broader than the anterior one (pl. 18, figs. 8–11). The cells had the quadrate arrangement with their long axes parallel, but in this material there was not the tendency for the anterior ends to diverge somewhat from one another as W. & G. S. West (1896) have described for their four-celled *G. lacustre*, and as Chodat (1902) has figured for *G. sociale*. Each cell in the colony was enclosed by a firm gelatinous envelope. When the colonies were viewed from above the only portions of the envelope visible were the short blunt processes which connected two abutting cells (fig. 8). When the colonies were seen in profile the envelope was seen to form a short rostrate projection at the anterior end of the cell (fig. 9). This firm envelope is usually the only one seen when living material is examined. If colonies are mounted in a dilute suspension of India ink a second gelatinous envelope of a much more watery consistency becomes evident (figs. 5, 6). In young colonies the outer sheath, which has a width approximately equal to the diameter of the cells, is not of uniform contour when seen from the side but follows the profile of the various cells in the colony.

Contrary to what is found in *G. pectorale* and *G. formosum* there was a very strong tendency for the individual cells to dissociate from one another in the material collected from Professor Mac Murphy's pool. W. & G. S. West (1896) have noted this same tendency in the four-celled form that they had under observation. Bock (1926) finds that cutting 16-celled colonies of *G. pectorale* into smaller pieces tends to accelerate asexual reproduction, and he ascribes the stimulation of reproduction to a severing of the fine cytoplasmic connections between the cells. In the case of *G. sociale* there was no particular evidence to show that the fragmentation of colonies accelerated the formation of daughter colonies. Single cells and two-celled fragments had the same wide gelatinous envelope as was found around four-celled colonies. This seems to show that the solitary cells arise by a fragmentation of the colony and not by a slipping out of isolated cells from the colonial envelope.

The formation of daugher colonies was repeatedly found both in iso-

lated cells and in cells which were united to form colonies. When colony formation took place in cells belonging to a colony there was an approximately simultaneous division of all four cells in the colony. After the young colonies were formed they escaped from the gelatinous envelope of the mother colony. Conditions were somewhat different when daughter colonies were formed by free-swimming isolated cells. These isolated cells gave rise to four-celled colonies in much the same fashion as in cells which were joined to one another, but the young colonies did not become separated from the firm gelatinous sheath that surrounded the mother cell. Instead, the firm sheath surrounding the mother cell remained embedded in the posterior end of the gelatinous envelope surrounding the new colony. Water mounts of young colonies usually showed the firm sheath of the mother cell a short distance from the posterior end of the colony and apparently unattached to it (fig. 9) but colonies mounted in dilute India ink showed that this effect was due to the very watery wide gelatinous envelope surrounding the colony (fig. 11). It is very probable that what Scherffel saw when he described *G. sacculiferum* was a *G. sociale* of this nature, and I am of the same opinion as Pascher (1927) that this species is to be included under *G. sociale*.

The *sacculiferum* type of colony may also be formed from cells belonging to colonies as well as from isolated cells. In this case the fragmentation of the mother colony takes place after the daughter colonies are formed.

STANFORD UNIVERSITY
CALIFORNIA

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Explanation of plates 17, 18

PLATE 17

Fig. 1. *Eudorina elegans* Ehrenberg (×400).

Fig. 2. *E. elegans*, female colony with antherozoids swimming through colonial envelope (×400).

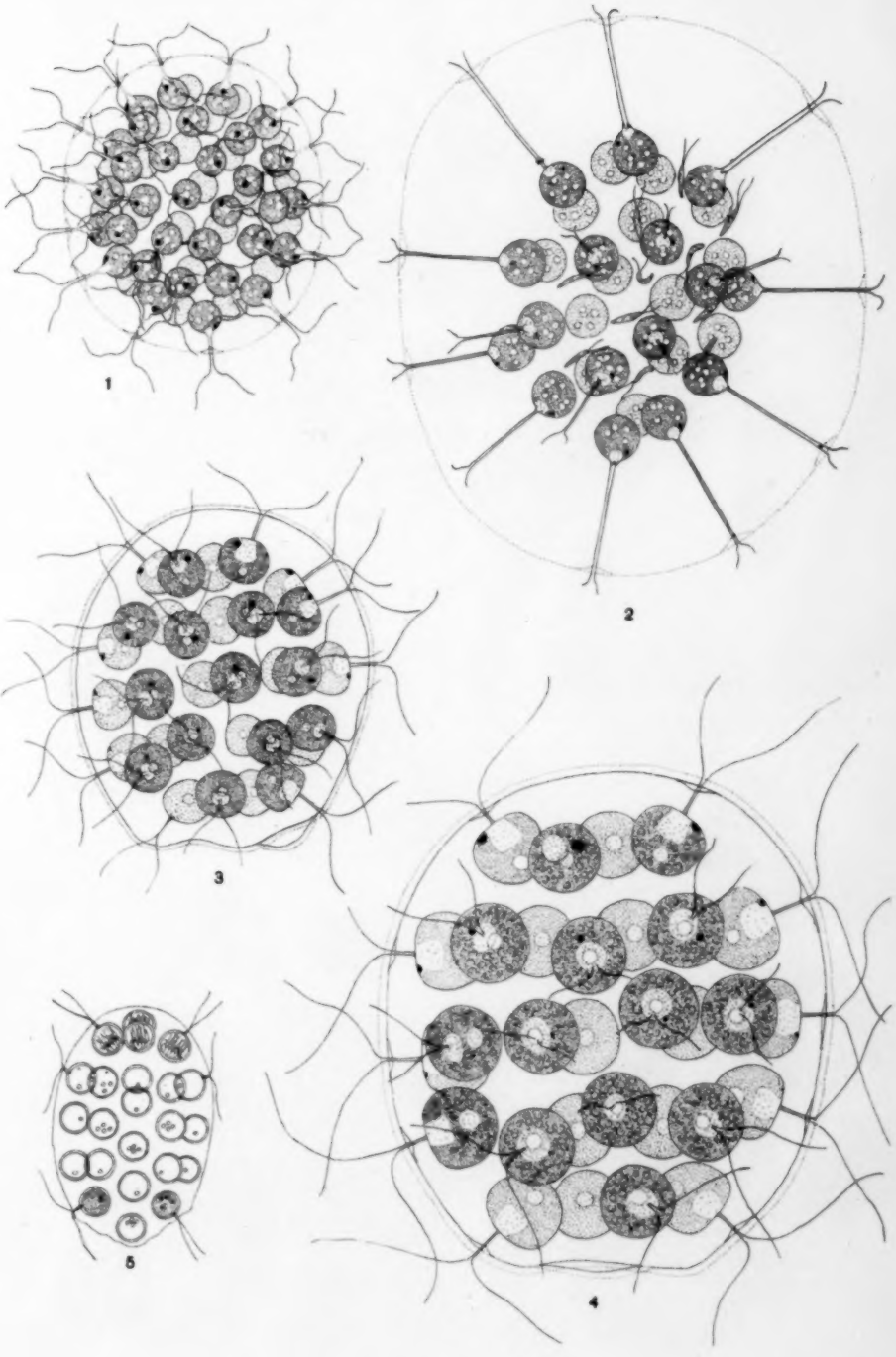
Figs. 3, 4. *E. unicocca* G. M. Smith from Stockton, California (×650).

Fig. 5. *E. Carteri* G. M. Smith (after Carter).

PLATE 18

Figs. 6, 7. *Pandorina charkowiensis* Korshikov from Stockton, California (×650).

Figs. 8–11. *Gonium sociale* (Duj.) Warming from Palo Alto, California (×650).



SMITH: VOLVOCALES

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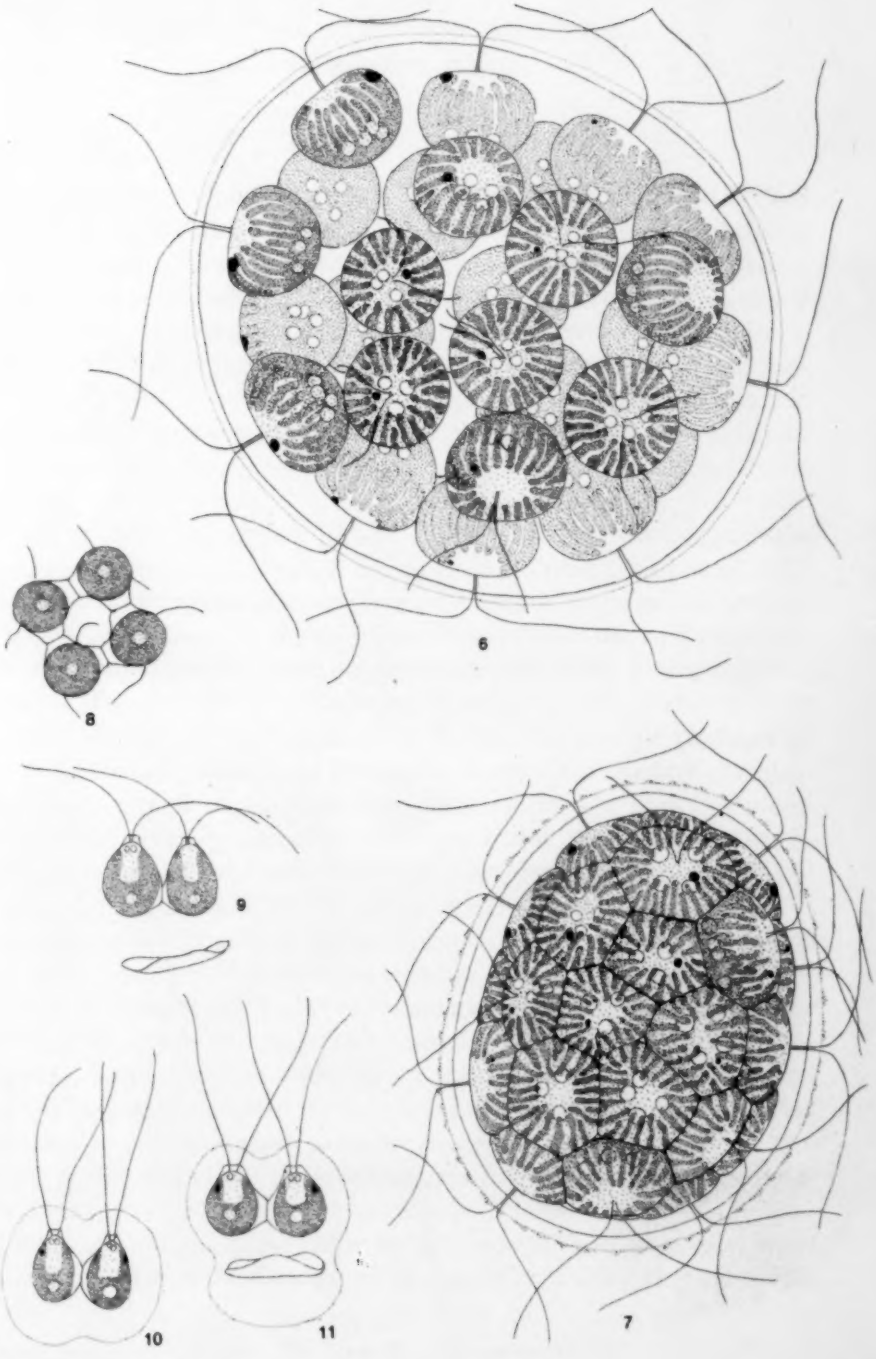

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The origin of the six-furrowed configuration of Dahlia pollen grains

ROGER P. WODEHOUSE

(WITH PLATE 19)

The pollen grains of *Dahlia* are unique among the Compositae in their possession of six germinal furrows. The prevailing number of furrows among the grains of the Compositae, and in fact with certain exceptions, throughout the dicotyledons, is three. Nevertheless there are encountered here and there, isolated groups of species, single species, or single individuals, which differ from their blood relatives in the very conspicuous character of the possession of supernumerary furrows. A notable example is that of *Dahlia*. The pollen grains of all species[1] and of all of the cultivated varieties that I have been able to examine are found to have uniformly six furrows (fig. 12).

It has already been shown (Wodehouse, 1929) that the prevailingly three-furrowed (tricolpate) type of pollen grain is directly associated with the tetrahedral arrangement of the four microspores in the pollen mother-cells, which is the usual arrangement in dicotyledons; and that other numerical configurations of furrows are associated with other arrangements in the tetrad. The prevailingly tetrahedral arrangement of pollen tetrads is unquestionably due, in the last analysis, to the ever present tendency among cells, whether single or in groups, to assume least surface configurations. Since this is so, any other arrangement of four cells in a group suggests somedisturbing influence. For this reason the meiotic stages in the pollen mother-cells of *Dahlia* were examined, with attention directed to the achromatic figures and spatial configuration of the daughter nuclei.

The first, or heterotypic, division offers nothing unusual (fig. 1). As the two groups of daughter chromosomes separate, the fibers of the central spindle are nearly straight (fig. 2), but as the daughter nuclei enter the telophase and reorganize, the fibers apparently become more numerous and the central spindle figure becomes wider in its equatorial region. These initial stages in phragmoplastic activity may persist for a longer or shorter period and the fibers generally show some thickening midway between the two daughter nuclei as if about to form a cell plate, but ultimately the phragmoplast disappears without completing cell division. The whole heterotypic division thus presents a picture which is typical of the dicotyledons in which the subsequent divisions of the mother-cell into four are simultaneous.

[1] *Dahlia pubescens* Brongn., *D. coccinea* Cav., *D. variabilis* Desf., *D. excelsa* Benth.

When the chromosomes are arranged on the equatorial plate in the second, or homeotypic, division, there is much irregularity in the orientation of the spindles. They may be in any relative position except end to end. Their axes may lie in planes at right angles to each other (fig. 4), but more often they tend to lie in the same plane (figs. 5, 6) and may even be exactly parallel and side by side. As the chromosomes separate and move towards the poles of the spindles, the connecting fibers are straight and have the appearance of being stretched taut between the two groups of nuclei (fig. 7), but when the nuclei enter the telophase and reorganize, the system of connecting fibers appears widened in its equatorial region, as in the first division, but without the appearance of the central thickening suggestive of cell plate formation (fig. 8). At about this time two, and only two, further spindles appear between the four nuclei of the second division (figs. 9, 10). The *Dahlia* tetrad is thus provided with four, instead of the usual six, connecting spindles. These four spindles, though easily distinguished, are less clearly defined than the spindles activly functioning in the nuclear divisions.

I have not been able to find in the literature an explanation of how the two additional spindles arise. The work of Devisé (1921) on the achromatic figures of the sporocytes of *Larix* offers some suggestion that they may be regarded as the reappearance of the heterotypic spindle split longitudinally into two halves. In the heterotypic division of *Larix*, when the spindle fibers fade, the cytoplasmic elements do not invade the spindle body: 'il s'est montré impénétrable à tout élement figuré et notament aux chondriosomes.' His figures show that this impenetrable space persists, dividing in two at the homeotypic division, and it is in these two spaces that the two accessory spindles come into view.

The position of the two additional spindles in the tetrad of *Dahlia* suggests that they represent two halves of the heterotypic spindle, but since the two spindles of the homeotypic division may be oriented in almost any direction relative to each other (figs. 4–8), it is apparently impossible for the heterotypic spindle to persist, in any tangible form, through the homeotypic division. Nevertheless, as the four nuclei of the second division become reorganized, they assume a more uniform arrangement than would be expected from the irregular orientation of the spindles by which they were produced, and this arrangement does not tend to be tetrahedral, and cannot, therefore, be attributed exclusively to a tendency towards least surface configuration; the four nuclei exhibit a strong tendency to lie all in the same plane, assuming a flat tetragonal form, which may be either square (fig. 9) or rhomboidal (fig. 10), and the mother-cells with their four nuclei in this arrangement are likewise flattened in the same plane. The four nu-

clei are, however, always equidistant along the axes of the connecting spindles, as if the latter were actually gauging the internuclear distance along these lines, or else were the expression of the forces which establish and maintain these intervals.

It is not the purpose of the present communication to discuss the much debated question of the nature or origin of spindles. The literature on this subject has been fully reviewed and discussed by a number of authors, notable among whom are Wilson (1925) and Sharp (1926). Though there is much disagreement among the different investigators, most seem to agree that the central spindle is something tangible, capable of exerting a pulling, pushing, or supporting effect upon the groups of daughter chromosomes or nuclei which it separates. Thus Yatsu (1909), in his studies upon the segmenting egg of *Cerebratulus*, states that 'The spindle fibers are made up of hyaloplasm more highly modified than that of the polar rays. The spindle may be removed as a whole . . . and retain its entity even after the egg is crushed.' Chambers and Sands (1923) showed that in pollen mother-cells of *Tradescantia*, the granular cytoplasm could be detached from the surface of the spindle. Devisé (1921), in his studies on the microsporocytes of *Larix*, found that the substance of the spindle is firmer than that of the cytoplasm. Chambers (1924) showed that the viscosity of the spindle is relatively high during metaphase but diminishes during telophase.

Soon after the appearance of the two additional spindles in the tetrad, quadripartition of the cell begins. This is accomplished by the process known as simultaneous furrowing, essentially as described by Farr (1916) for the tetrads of *Nicotiana*, except as modified by the non-tetrahedral placement of the daughter nuclei of the *Dahlia* tetrads and the resultant flattened shape of the cells. The stresses involved are of the greatest interest, and are not fully described by Farr. It is as though each nucleus were a center of contraction, about which the colloidal cytoplasmic mass tends to round up. We get a visible presentation of Sachs' conception of the 'energid.' Each nucleus dominates its own fourth of the cytoplasm. The furrows which result from this movement of aggregation are to be seen first as two four-cornered depressions forming on opposite sides of the pollen mother-cell midway between the four daughter nuclei. Growing inwards these finally meet in the center, forming a four cornered hole with concave sides, through the center of the tetrad, which becomes filled with the homogeneous, apparently hydrolyzed, material of the pollen mother-cell wall (fig. 11). This leaves each nucleus in its own cell but still connected by two broad channels (pit connections) with its two lateral neighbors of the tetrad; and each of these channels encloses the remains of the poorly developed connecting spindle or phragmoplast. At the time when the fur-

rowing results in forming the hole between the four nuclei described above, the peripheral surface of the cell is cut by four furrows, one between each pair of nuclei and opposite each of the four corners of the central opening (fig. 11). Upon changing the focus of the microscope these furrows can be followed and shown to be annular constrictions encircling the pit connections. These constrictions become progressively deeper and finally cut through between the daughter nuclei, bisecting the remains of their contained phragmoplasts, and thus completely separate the four daughter cells.

Immediately upon their separation the daughter cells lose all trace of the pit connections; the contraction of the cytoplasm ceases, it becomes flaccid and the four cells flatten slightly against each other, thus tending to conform once more to the general curvature of the group as a whole. At this stage these four cells, or sporocytes, are smooth quadrants. Their walls now begin to thicken and the spines appear as minute papillae. With this thickening they become more turgid and rounded, exhibiting no visible suggestion of their former connections and asymmetrical origin. Then, and not until then, do the germinal furrows become evident.

As we have already seen, the furrows are six in number. They are equally spaced on the surface of the grain and are so oriented that their long axes converge in threes towards four equally spaced centers. Such an arrangement may be likened to a tetrahedron, the furrow axes corresponding in spatial configuration to its six edges and the four centers of convergence to its four solid angles.

In the sequence of events described above, the four daughter nuclei were considered in the square arrangement. Frequently the daughter nuclei may likewise form a rhomboidal figure with two of the nuclei very close, sometimes nearly touching (fig. 10), but there are no spindles crossing between diagonally opposite nuclei, either along the long or the short diagonals of such a rhombus. In such an arrangement the only spindles that are in evidence are the four which lie along the sides of the rhombus. Frequently the daughter nuclei do not all lie in the same plane, tending sometimes to approach the tetrahedral arrangement. In the majority of cases such tetrads are obviously only slightly modified from the flattened tetragonal arrangement by the displacement of one or two of the nuclei above or below the plane of the others, and not materially affecting the arrangement. Occasionally, however, such a displacement is carried so far that the four nuclei actually assume the tetrahedral arrangement. Such a complete displacement is quite unusual, but when it does occur it does not modify the process of furrowing in any way. The result of the furrowing is the same as when the four daughter nuclei lie all in the same plane; for only four pit connections are formed.

It appears that the usual flat tetragonal placement of the four daughter nuclei in the *Dahlia* tetrad is due to, or is at least associated with, the presence of four phragmoplasts. Such an arrangement, however, is in conflict with the tendency towards least surface configuration which is the property of all cells and groups of cells. Consequently it is not surprising to find some tetrads in which the universal tendency towards least surface configuration, leading to the tetrahedral arrangement, has prevailed over the very special tendency towards the tetragonal arrangement. Nevertheless the result of the subsequent furrowing is always the same, leaving the daughter cells, just before final separation, joined to their neighbors through two instead of the usual three pit connections.

I have already shown (Wodehouse, 1930) that two points of contact between cells in a tetrad may cause, in the mature pollen grain, the formation of any one of a long series of furrow configurations. The actual number of furrows and their configurations depends principally upon the distance apart of the two final contact points between the daughter cells; but the most favored configurations are those in which the furrows correspond, in their position and their orientation, to the edges of certain geometrical solids, conspicuous among which are those perfect polyhedra which have three equal angles at each of their vertices, the tetrahedron, cube, and pentagonal dodecahedron.[2] In those tetrads in which the arrangement of the nuclei is approximately square the contact points tend to be one quarter of the circumference apart, which interval corresponds to the central points of the six edges of a tetrahedron, and consequently makes possible the development of six furrows, two at the two points of contact and four more so arranged that they complete the symmetrical configuration which fits the interval established by the original two points, and in this case is the tetrahedron.

[2] The analogy between the various furrow configurations on the surface of pollen grains, and certain polyhedra was first pointed out by Von Mohl (1835) and further elaborated by Fritzsche (1837). Von Mohl, centering his attention on the polygonal areas bounded by the furrows, rather than upon the furrows themselves, regarded these areas as corresponding to the faces of the polyhedra; consequently the furrows correspond to the edges of the polyhedra, and the apertures, when present, become the central points of the edges of the polyhedra. Other investigators, for example Fritzsche in his description of the grains of *Basella alba*, and Tammes in his studies on the origin of the germinal apertures of pollen grains, centering their attention on the pores, to the exclusion of both the furrows and the polygonal areas which they bound, have regarded the apertures, and consequently their furrows when present, as corresponding to the centers of the faces of the polyhedra. It seems to me that the former view is more enlightening, because, if the pores are regarded as the middle points of the edges of polyhedra, the orientation of the furrows, when present, is at once determined by the same analogy, since they correspond in direction to the edges of the polyhedra. On the other

It is true that a large proportion of the *Dahlia* tetrads do assume the square arrangement, or some approximation to it. Nevertheless, as we have already seen, some of the tetrads are distinctly rhomboidal. Such an arrangement would obviously not result in the contact points being placed ninety degrees apart. Those cells formed at the opposite ends of the long diagonals of the rhombus would have their contact points less than ninety degrees apart, while those at the ends of the short diagonals would have them more than ninety degrees apart. From such a tetrad we should therefore expect two of the grains to develop their apertures closer than demanded by the tetrahedral configuration, and two of them to develop them farther apart. Indeed in the grains of *Salpiglossis*, which are shed united in their tetrads, the latter is actually sometimes the case. Occasionally cells are found making only two points of contact with their neighbors; such cells develop their furrows in the ordinary tricolpate configuration, when the two points are about one third of the circumference apart; but they develop four or six furrows in the tetrahedral configuration if the points of contact are only about one quarter of the circumference apart. In the grains of *Dahlia*, on the contrary, such deviations from the ninety degree angle fail to alter the tetrahedral configuration.

Furthermore the distance apart of the contact points, no matter how accurately gauged, can only determine the spatial configuration of the fur-

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hand, if the pores are regarded as corresponding to the centers of the faces of the polyhedra, while providing a convenient means of discussing the position of the pores, this analogy leaves the furrows, if present, directionally unfixed in the planes of the faces of the polyhedron. The orientation of the furrows appears to be the most important part of such an analogy because the observed facts have shown that the furrow configurations are a fundamental part of the pollen-grain structure, and obey mathematical laws just as exacting as those governing the placement of the pores. In fact there is ground for believing that the actual number and distribution of the pores is often secondary to the furrow configurations. When the furrows are regarded as corresponding to the edges of the polyhedra, the comparison of pollen grains with polyhedra is something more than an analogy because the series of observed furrow configurations is found to correspond closely to the series of theoretically possible polyhedra (Wodehouse, 1930).

Moreover I suspect that there is a physical basis, which we have not yet been quite able to uncover, for regarding the furrows as corresponding to the edges rather than to the faces of polyhedra. For example the tetrahedron is the simplest possible regular polyhedron, and it is well known that when a sphere contracts, as for example a blown glass bulb, it tends to assume the form of a tetrahedron; and this figure corresponds to the commonest furrow configuration, other than the ordinary tricolpate form, if the six edges of the tetrahedron are regarded as analagous to the furrows of the grain; but if its four faces be regarded as corresponding to as many pores, the tetrahedron represents no known pollen-grain configuration.

rows, and it so happens in the grains of *Salpiglossis*, and many others, that the tetrahedral furrow configuration is almost as likely to be represented by only four of its six furrows, two of the furrows failing to develop. Such I have never found to be the case in the grains of *Dahlia*. The rigid uniformity of the development of the tetrahedral furrow configuration, always with its full complement of six furrows, arising from two points of contact which may be irregular in arrangement, is a fact of curious interest and deserving of further consideration.

With pollen grains, as well as with all cells and all organisms, there are two distinct factors controlling their development—heredity and environment. I have already pointed out (Wodehouse, 1929) that the majority of pollen-grain characters may be assigned definitely to one category or the other. And on this basis certain characters may be designated as emphytic (inherited) and others as haptotypic (environmental). In the case of *Dahlia* pollen grains, as in most others, the texture, the nature of the spines, such as their length and distance apart, and the length of the furrows are unquestionably purely emphytic characters. The fact that the grains are not tricolpate—that is to say, with three furrows meridionally arranged, as is more usual in dicotyledonous pollen grains—is purely a haptotypic character, arising as it does, out of a condition of the internal environment, viz., two, instead of the usual three, contact points; but the fact that two contact points results, in the *Dahlia*, always in the development of six furrows rather than any of the other possible numbers is again emphytic, a character inherent in the cell.

This observation shows that the line between emphytic and haptotypic in cells becomes at times vague, just as it does between hereditary and environmental in plants and animals. There are many characters which are at times distinctly hereditary and at others distinctly environmental. Such, for example, is the reddish coloring sometimes seen in maize plants growing in open sunny places. This character is strictly hereditary in the sense that it is transmitted from generation to generation in typically Mendelian fashion, but it is environmental in the sense that it can only develop if the plants are growing in full sunlight.[3]

In the pollen-grain forms of many species the furrow configuration is apparently almost entirely haptotypic, depending principally upon the number and distance apart of the contact points. Thus it happens that when grains are found with four or six furrows in the tetrahedral configuration, there are generally also found in the same pollen other grains with higher numbers of furrows in other configurations. In such cases the grains are generally various in size, and the larger grains tend to have the larger

[3] This and other such characters are discussed by Jennings (1930).

numbers of furrows. Indeed Tammes (1930) has recently shown by statistical methods that among the species of *Oenothera* and others there is a rough correlation between the size of the grain and the number of its apertures, the number of apertures on a grain tending to be directly proportional to the area of its surface. The variation of the number of apertures in relation to the size of the grain follows a discontinuous course almost in conformity with the laws governing the number of possible equidistant points on the surface of a sphere. From this he deduces the law that each germinal aperture must be surrounded by a definite area which is characteristic in extent for the species. This is apparently true in the case of *Dahlia* pollen. Since the grains are extremely uniform in size, the fixing of the distance apart of the pores would result in a fixing of the number on the surface. This being so, we come to the conclusion that the uniformly hexacolpate furrow configuration of *Dahlia* pollen grains is hereditary and therefore emphytic, governed, as it is, by two hereditary factors, the uniformity of the size of the grains and the fixity of the distance apart of the apertures.

SUMMARY AND CONCLUSIONS

Dahlia pollen grains are conspicuous among those of the Compositae for their possession of six germinal apertures instead of the more usual three. Associated with this is the equally exceptional fact that the four nuclei of the homoeotypic division have a tendency to lie in one plane, presenting a square or rhomboidal arrangement, instead of the more usual tetrahedral arrangement, and the four nuclei are connected by four instead of the more usual six connecting spindles. These phragmoplasts are the expression of the forces which tend to place and hold the four daughter nuclei of the tetrad in the position of the angles of a square or rhombus, rather than in the positions of the angles of a tetrahedron.

Quadripartition is by furrowing, ending by constricting across the four connecting phragmoplasts, thus giving to each daughter cell only two instead of the more usual three points of contact. These two points determine the position of the six symmetrically placed furrows in the tetrahedral configuration.

I am indebted to the San Francisco Dahlia Society for the use of the preparations upon which these observations were made. The slides were made by Dr. Donald A. Johansen of Stanford University, and it is owing to their exceptional quality that such difficult observations as those of the spindle fibers passing through the pit connections were possible.

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Explanation of plate 19

All figures were drawn free hand from observations made with a Zeiss 3 mm. apochromatic objective, n.a. 1.4, and paired 15× compensating oculars giving stereoscopic vision, total magnification 900. Measurements were made with a 2 mm. apochromatic objective, n.a. 1.3, and a 20× compensating ocular, total magnification 1800.

Figs. 1–11 show various stages of the meiotic divisions of the pollen mother-cells of *Dahlia variabilis* Desf., while fig. 12 is of a mature pollen grain of *Dahlia excelsa* Benth.

Fig. 1. Metaphase of the first or heterotypic division.

Fig. 2. Anaphase of the heterotypic division.

Fig. 3. Telophase of the heterotypic division.

Figs. 4, 5, 6. Metaphase of the second or homeotypic division showing random orientation of the spindles.

Fig. 7. Anaphase of the homeotypic division.

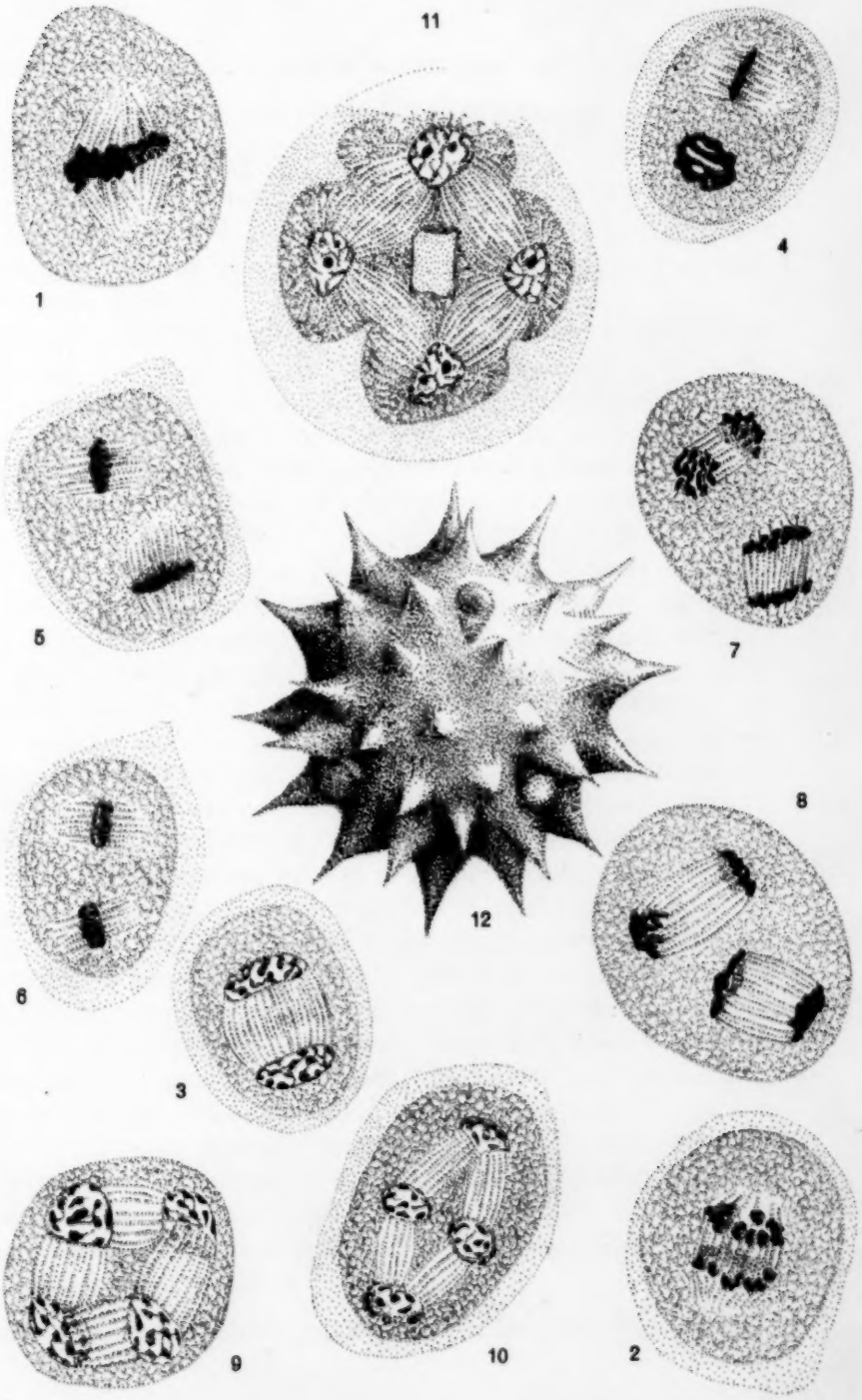
Fig. 8. Late anaphase or early telophase of the homeotypic division.

Fig. 9. Telophase of the homeotypic division. The four daughter nuclei are joined by four connecting spindles or phragmoplasts. Their arrangement is square.

Fig. 10. As in fig. 9, except that the arrangement of the daughter nuclei is rhomboidal.

Fig. 11. Quadripartition by furrowing. Division starts by the formation of two depressions on opposite sides of the tetrad, between the four nuclei and ends by constricting across the four phragmoplasts.

Fig. 12. Mature pollen grain of *Dahlia excelsa* Benth. showing three of its six germinal furrows converging towards the uppermost point on the hemisphere. There are three more furrows on the lower hemisphere alternating with these and with their axes oriented tangentially. The form of this grain is the same as that of *D. variabilis*, except that the furrows in this are slightly longer and more sharply defined.



WODEHOUSE: DAHLIA POLLEN GRAINS

Bactrophora irregularis, a new brown alga from Australia

JOSEPHINE E. TILDEN AND ANNA PARKER FESSENDEN

(WITH PLATES 20, 21)

The genus *Bactrophora* was established by J. G. Agardh (1880, p. 22-24) who had in mind the resemblance of the peripheral assimilatory filaments of the plants to the crook or crosier of a bishop (Greek: *βάκτρον*, a staff, a rod, and *φορέω*, to bear).

Agardh included three species in the genus *Bactrophora*, all of them described from specimens brought from the southwestern and southeastern shores of Australia by William Henry Harvey,[1] who collected in that country between January 7, 1854 and June 15, 1855. *B. Filum* (Harvey) J. Agardh was found in King George's Sound, Western Australia by Harvey (1855) and briefly described by him as *Mesogloia filum;* it was later reported by Sonder (1880, p. 9) from Queenscliff, Victoria. *B. vermicularis* J. Agardh was collected at Port Fairy, Victoria by Harvey, and at Orford, Tasmania by Lady Meredith. The third species, *B. nigrescens* (Harvey) J. Agardh, was said to be often attached to *Zostera*, and the localities given are Georgetown, Tasmania, where it was collected by R. Gunn and by Harvey (1859, p. 292–293), Western Port, Victoria, by Harvey; and later reported 'at or near Port Phillip Heads and Western Port,' Victoria, by J. B. Wilson (1892, p. 163). Probably Wilson did not collect the alga but is merely referring to Harvey's collection.

From a study of the history of *Bactrophora*, it seems probable that few plants belonging to the genus have ever been collected, and that, aside from Agardh, who examined their morphological characters and described them, no one has done systematic or morphological work on the genus. No measurements have been given for the cells of the various parts of the frond. As far as is known to us, only two figures are in existence, one of *B. nigrescens* (as *Cladosiphon nigrescens* Harv.) shown by Kützing (1859, *pl. 1, fig. 2*) and one of *B. Filum* (the type species) by Agardh (1880, *pl. 1, fig. 4*). For these reasons the following account of what seems to be a fourth species may be of interest, especially to students of the Phaeophyceae.

The new species here proposed was collected by Miss Tilden at Basin Bay, Kiama, New South Wales, Australia, on September 24, 1912. The plants were found growing on rocks. They were of a light brown color and were soft and slimy to the touch.

[1] The three species of Agardh are based on Harvey's Alg. Austr. Exsic. nos. 91 D, 92, and 94.

A typical plant consists of an irregularly branched frond, attenuated toward the base, where it springs from a small flat disc-shaped holdfast. In the largest frond examined the width just above the holdfast was 0.5 microns and the greatest width was 2.5 microns, while the length was 13.5 cm. The branches arise from any point on the frond in no definite order. The largest branches measure 1 mm. in breadth and 5 cm. in length, and are slightly attenuated toward the tip. The lower younger branches are very short, slightly wider than the older ones, and are blunt or rounded off at the tip. Upon closer examination the frond is found to be composed of a colorless tubular jelly-like axis, covered with very short brown 'hairs,' which are more abundant in certain portions, thus giving to the frond varying shades of color.

MINUTE STRUCTURE OF THE FROND

No examination was made of the basal disc, as but one holdfast was found in the material at hand, and it was not deemed wise to mutilate the only perfect specimen in the collection.

The interior of the plant is composed of colorless, elongated, slightly branched and anastomosing multicellular filaments (pl. 20, figs. 5, 6) which take a longitudinal course through the frond. The central portion of the adult plant is practically hollow, the axial filaments forming a loosely connected layer surrounding the central cavity (fig. 8). From the exterior of this layer arise many stalked fascicles of peripheral assimilatory filaments (figs. 4, 10, 11) which grow out obliquely or at right angles to the longitudinal filaments.

The axial filaments are of three sizes (fig. 5), the broadest and middle-sized ones giving rise to the narrowest as branches. The cells of the broadest filaments (32–64×120–260 microns) are inflated at the middle and slightly contracted at the ends, where they are frequently joined to much narrower cells, thus giving an attenuated appearance to the filaments. The middle-sized filaments are more numerous than the broad ones and in these anastomosis most frequently occurs (fig. 6). They are composed of cells 24 microns wide and 120 microns long.

The smallest in size of the axial filaments are the most abundant. They arise as branches of the middle-sized filaments, and also from the base of the stalk of the fascicles of peripheral assimilatory filaments (figs. 2, 3, 4), at their point of attachment to the longitudinal parallel filaments. It is these smallest branches, whose cells range from 4–6 microns in diameter and from 100–115 microns in length, that grow downward in the frond and appear rhizoidal in character. They often depart from the tubular layer of filaments and make their way into the cavity in the center of the frond.

At the tip of the frond, or at the tip of a branch, these rhizoids, 120 microns or more in length, are seen in various stages of development.

The cells of the axial filaments contain little protoplasm, apparently, and practically no pigment material is present except in the outermost filaments from which the assimilatory threads arise.

In a transverse section through the frond (fig. 7), practically all of the axial filaments appear in cross section. Those near the periphery, however, are seen running lengthwise of the frond and terminating in assimilatory threads. The hollow interior is bordered by a layer made up chiefly of the largest of the filaments. The same structure can be made out in the longitudinal section (fig. 8). Here the axial filaments all appear running longitudinally and parallel to each other, on either side of the central cavity. Toward the exterior of the frond they turn outwards and give rise to peripheral filaments.

From observation of the axial filaments it might seem that the middle-sized were the primary filaments. Of course it is possible that they may increase in size, thus developing into the largest and oldest filaments, and in branching give rise to the smallest as well as to the peripheral filaments. This view is somewhat substantiated by an examination of the tips of the fronds, where there is found to be a large central cavity bounded by a few longitudinal, parallel, middle-sized filaments, which give rise to the peripheral fascicles and rizoidal branches.

The peripheral assimilatory filaments are borne in stalked fascicles (figs. 4, 11) and it is these that give to the frond its slightly hairy appearance. The average length of these fascicles from the top of the stalk to the apices of the branches is 200 microns. The branches grow out at about the same point on the stalk, and one cell may sometimes give rise to several branches. The peripheral filaments are attenuated toward the base, swollen or thickened and moniliform at the apex, and slightly incurved. They are composed of from 10 to 25 cells each. The apical cells have a greater diameter than the other cells of the filament. In some cases they are broader than long (20×12 microns) (fig. 9), while at other times they are longer than wide (12×16 microns) (fig. 11).

The cells in the middle of the filament are square in outline (8–12×8–12 microns), while the basal cells are oblong (4–6×8 microns). The apical cell is usually slightly larger than the cells below it. The swollen apical cells are divided usually but once, longitudinally or transversely (figs. 10, 12) (12–16×2–3 microns). Altogether, they resemble somewhat those described for *B. vermicularis*. The swollen cells, doubtless, add to the amount of curvature of the filaments. The moniliform appearance of the filaments

is more pronounced on the outer side of the curve, and here there sometimes occurs a one-celled branch.

The contents of the swollen cells are quite similar to the chromatophores in the other vegetative cells (fig. 9).

The peripheral assimilatory filaments appear as if inrolled upon themselves, as it were, so that they resemble, superficially, the circinate vernation of the fern leaf. This fact gave Agardh the opportunity of bestowing upon this genus a very fitting name, since the resemblance to a bishop's crosier is most striking (figs. 4, 10, 12).

In addition to the peripheral assimilatory filaments, a few long colorless hairs, or paraphyses, arise in the fascicles (fig. 4) and extend far out beyond the assimilatory threads. They are attenuated at the base and are composed of cells which vary in size (4×4 microns at the base; 8×32 microns at the top). They are usually broken off, leaving blunt ends.

REPRODUCTION

Agardh and others believed that the swollen cells of the assimilatory filaments contained reproductive bodies, and 'unilocular' and 'plurilocular sporangia' have been reported for the genus *Bactrophora*. Recent investigations lead us to believe that the gametophyte in the Chordariaceae is still to be discovered.

The plants studied are sporophytes. Unicellular ('unilocular') sporangia are borne at the bases of the peripheral assimilatory filaments where these arise from the stalk of the fascicle (figs. 4, 11, 13). The sporangia are sessile and are usually surrounded by peripheral filaments which curve around in such a manner as to enclose them partially. The sporangia are clavate to obovate in shape and the older ones are much swollen. They vary considerably in size, ranging from 8 to 40 microns in diameter and from 32 to 104 microns in length. The contents, for the most part, are finely granular and without definite arrangement within the hyaline sporangium wall, but occasionally there is an appearance as of small spheres closely packed together. The few empty sporangia seen were open at the apex and torn longitudinally (fig. 14). These structures in all probability are true sporangia, and the swollen terminal cells of the assimilatory filaments—the 'trichosporangia' of Agardh—are *not* plurilocular sporangia. The assimilatory filaments are purely vegetative structures.

GROWTH OF THE FROND

The mode of growth in the family Chordariaceae is known as subapical. The writers found no special region of growth in the axial filaments in any portion of the plant, except at the apex of a teased out branch, where the

presence of short cells seemed to indicate that growth occurs immediately below the apex of these filaments.

The growth of the peripheral filaments does not seem to be restricted to any particular portion, since both middle and apical cells were found in process of division. The rhizoidal filaments seem to grow basipetally, pushing downward in the frond. This is indicated by the presence of short, recently divided cells at their bases. The paraphyses, also, which occur among the peripheral assimilatory filaments, grow in length by division of cells at the base.

Bactrophora irregularis sp. nov. Fronde cylindracea, ramosa, ramis simplicibus, irregulariter egredientibus ex omni parte frondis; ramis longioribus parce attenuatis, brevioribus haud attenuatis, obtusis; filis axialibus majoribus 32–64μ diam., minoribus 4–6μ latis; filis periphericis ad 200μ longis; sporangiis 8–40μ diam., 32–104μ longis.

Hab. ad scopulos, Basin Bay, Kiama, New South Wales, Australia. 24 September 1912 (*Tilden 7093 B*).

Frond cylindrical, branched; branches simple, arising irregularly from any part of the frond; longer branches scarcely attenuated, shorter ones not at all attenuated, blunt at the apices; larger axial filaments 32–64μ in diameter, smaller ones 4–6μ in diameter; peripheral filaments up to 200μ in length; sporangia 8–40μ in diameter, 32–104μ in length.

CLASSIFICATION

Bactrophora irregularis is referable to the family Chordariaceae as described by J. G. Agardh, since the frond is composed of filaments which run through it in a longitudinal direction, giving off peripheral assimilatory branches. At this point Agardh and Kjellman differ in their classification. Agardh separates the genera according to the relation of the peripheral branches to the confining gelatin. Kjellman, on the other hand, uses the mode of growth as the distinguishing character in setting off the genera in the family. In the material studied it was impossible to determine either point. Kjellman (1893, p. 226) himself says, in describing the genus *Bactrophora*, 'Sprossaufbau nicht bekannt.' Omitting these two points, the plant corresponds in all other respects to the descriptions and keys leading to the genus *Bactrophora* in both classifications.

As stated above, Agardh included three species in the genus *Bactrophora*, and they have been retained by De Toni (1891, 1895). From *B. Filum* the new species differs in the fact that it has no distinct stipe; that it is much branched; that the basal cells of the peripheral filaments do not give off twin branches; that the peripheral filaments are less curved; and that the size and shape of the cells of these filaments do not at all correspond to those in Agardh's illustration. In the case of *B. vermicularis*, the

new species fails to correspond in the method of branching and in the number and shape of the branches. Nor does it resemble *B. nigrescens* in the method of branching or in the shape of the fertile peripheral filaments, according to Agardh's description and the drawing of Kützing.

All preparations for the study of the material were made by Miss Fessenden, as well as the drawings in the plates.

It is hoped that someone who has access to the herbarium material of W. H. Harvey may soon undertake a study of the entire genus *Bactrophora*.

DEPARTMENT OF BOTANY
UNIVERSITY OF MINNESOTA
MINNEAPOLIS

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Explanation of plates 20, 21

PLATE 20

Fig. 1. Frond of *Bactrophora irregularis*.

Fig. 2. Stalks of peripheral assimilatory filaments branching from axial filaments. Rhizoidal branches growing down from end of stalk at the point from which the peripheral filaments arise.

Fig. 3. Detail of rhizoidal branches shown in figure 2.

Fig. 4. A fascicle of assimilatory filaments with stalk and rhizoidal branch and long colorless paraphyses.

Fig. 5. A group of axial filaments showing the variation in size.

Fig. 6. Anastomosing axial filaments.

Fig. 7. Part of a transverse section through a small frond, showing hollow center, cross cut longitudinal filaments, and peripheral filaments.

PLATE 21

Fig. 8. Longitudinal section through a small frond, showing hollow central region, axial filaments running longitudinally and parallel, and peripheral filaments arising obliquely.

Fig. 9. Apical cells of a peripheral assimilatory filament, showing protoplasmic contents.

Fig. 10. A fascicle of filaments showing longitudinal and transverse divisions of the apical cells.

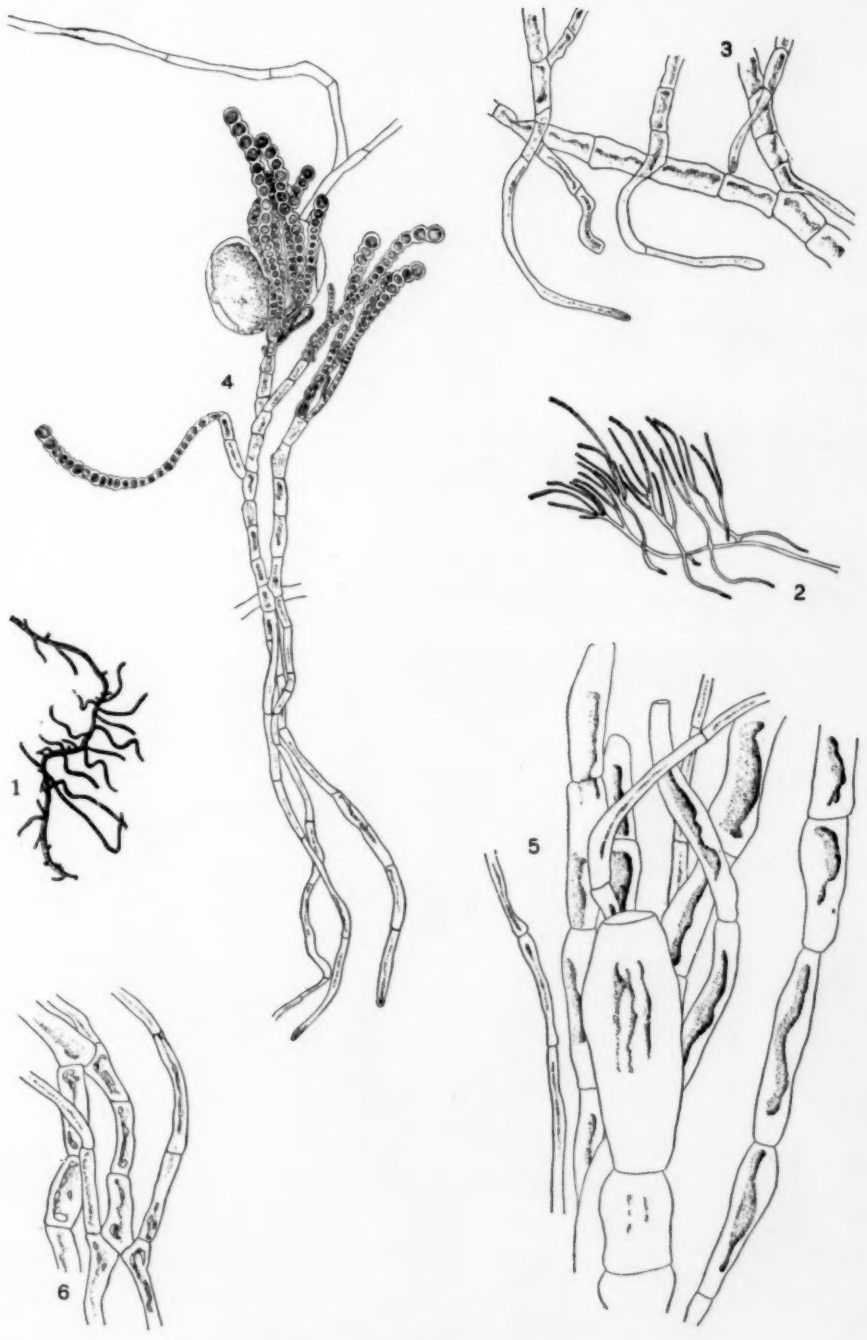
Fig. 11. A fascicle of curved assimilatory filaments showing one sporangium.

Fig. 12. A small, much curved assimilatory filament.

Fig. 13. Mature sporangia surrounded by short assimilatory filaments.

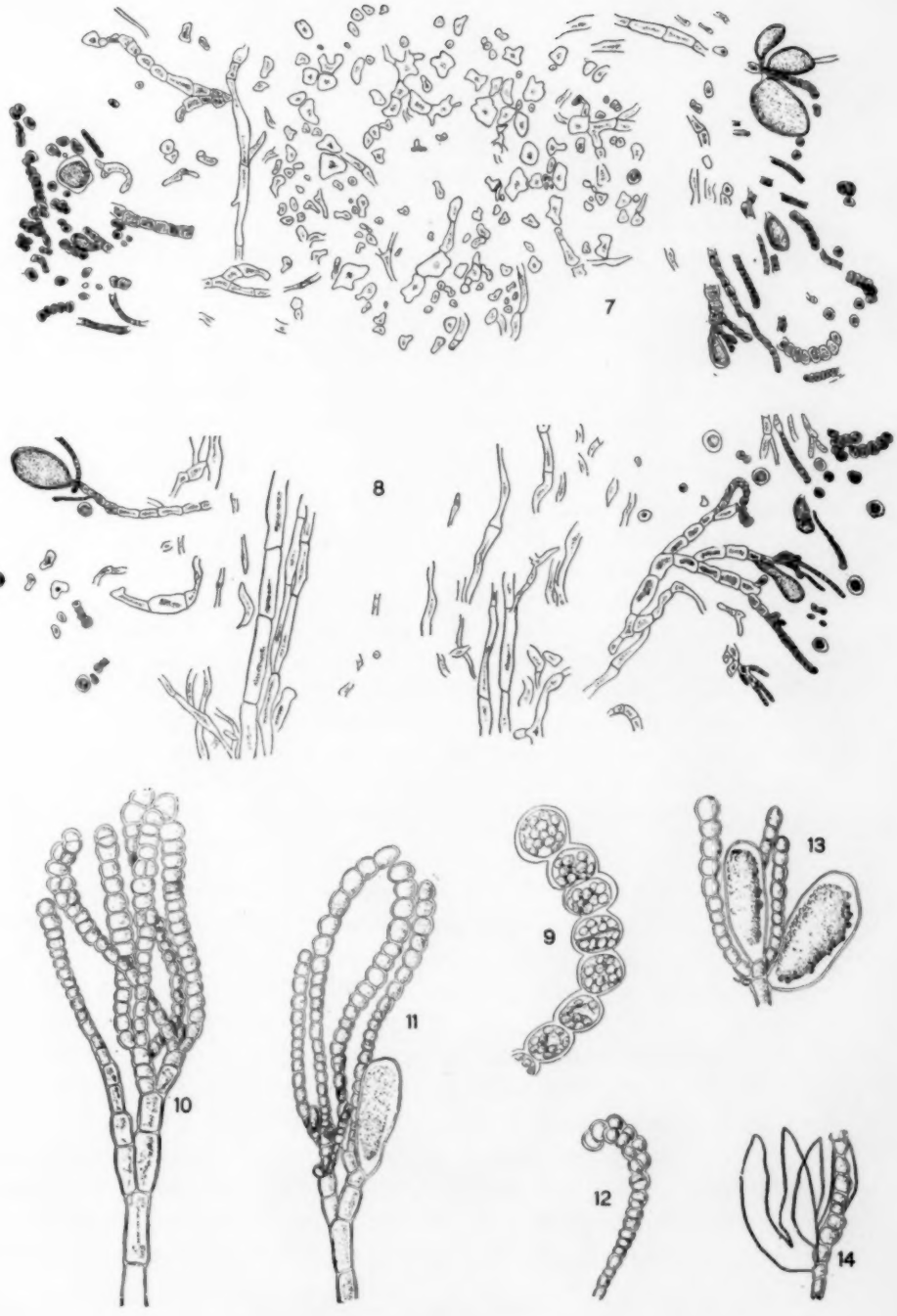
Fig. 14. Empty sporangia.

All drawings were made with the aid of the camera lucida.



BACTROPHORA IRREGULARIS TILDEN & FESSENDEN

UNIV. OF MICH.



BACTROPHORA IRREGULARIS TILDEN & FESSENDEN

UNIV OF MICH

Two genera of algae new to Bermuda[1]

LAWRENCE ROGERS BLINKS AND ANNE HOF BLINKS

(WITH PLATES 22, 23)

The present paper reports two genera new to the algal flora of Bermuda. One of these, *Halicystis*, has been previously unrecorded from the western Atlantic in its proper identity, and the other, *Corynomorpha*, is known in America only from the collection of Harvey made eighty years ago in Florida, and of Mazé and Schramm[2] in Guadeloupe. Since the previous collections of both plants were of stranded material, these are the first records of the growing organisms in the western Atlantic.

Halicystis Osterhoutii n. sp. (pl. 22, 23, figs. 9–12, text fig. 18)

Plants always single cells, from less than 1 mm. to over 3 cm. in diameter; multinucleate, unbranched, spherical to pyriform, attached to substratum (usually *Lithothamnium*) by a narrow pedicel. Cell wall smooth, thin, transparent, tough and extensible, not obviously laminated. Protoplasm lining the wall in a thin layer. Chloroplasts lenticular, rounded or irregularly angular, *possessing one or more pyrenoids*. Nuclei irregularly scattered. Megazoospores 10–15μ long, 9–12μ wide, but mostly *nearly spherical, 11μ in diameter*, biciliate, without eye spot; formed in dark crenate plates at or near apex of cells, escaping through clear papillae. Microzoospores (4μ ? in diameter) formed in pale, opaque plates. Type material: Herb. A. Hof Blinks, Coll. A. H. Blinks, Great Sound, Bermuda, April 23, 1929; duplicates in herb. New York Botanical Garden.

The specific name is proposed in tribute to Dr. W. J. V. Osterhout, who has studied the general physiology of algae for over thirty years, and who published, with M. J. Dorcas, the first chemical analysis of the cell sap of *Halicystis*, under the then current name of *Valonia ventricosa*. (Osterhout and Dorcas, 1925.)

Halicystis has one of the simplest structures found in the Siphonales. The plant body consists only of an expanded multinucleate cell attached by a narrow neck to a small rhizoidal portion imbedded in the thallus of some coralline alga. There has previously been but one well established species, *H. ovalis* (Lyngb.) Aresch. '*H. parvula*,' reported by Murray (1893) as named by Schmitz from the Mediterranean, apparently resembles the proposed Bermuda species, but there has been no adequate

[1] Contributions from the Bermuda Biological Station for Research No. 162.

[2] MAZÉ, H., AND A. SCHRAMM. Algues de la Guadeloupe. Ed. 2. p. 158. Basse-Terre, 1870–77.

description of it and the name seems of doubtful validity. Until the very recent studies by Smith (1930) the morphology and reproduction of the genus were known only from the excellent work of Kuckuck (1907). *Halicystis* has been included in the Protosiphonaceae, Valoniaceae, and, most recently, in a special family established by Smith, the Halicystaceae. It was frequently assigned to *Valonia*, until Kuckuck's work showed it to have a very different type of reproduction from that genus. And as *Valonia ovalis* it was reported by Saunders (1899), who first collected it in America (Point Lobos, Monterey peninsula, California, 1896). Subsequent collections on the Pacific coast were very few (see Setchell and Gardner, 1920, p. 154), until the recent survey of Hollenberg disclosed several stations near Monterey (Smith, 1930). We are indebted to Dr. Tracy E. Hazen for specimens of *H. ovalis* from that region collected in July, 1930. The European collections are from such varied regions as the North Sea, the Clyde Sea, and the Bay of Biscay (Murray, 1893). Feldmann (1929) has found *H. ovalis* recently in the Mediterranean, both on the French coast, and in Algeria (personal communication).

Until 1927, *Halicystis* was apparently unrecorded from eastern America. In that year one of us reported specimens from the Atlantic (Bermuda), and from the Gulf of Mexico (Tortugas, Florida) (Blinks, 1927). These had been examined and identified by Dr. Marshall A. Howe, who also agreed to a change in identification of material in the New York Botanical Garden herbarium. These were specimens of the plant, frequently washed up on Bermuda beaches, known as 'sea-bottles' from the pale green single cells filled with clear sap, which spurts out with some force when the wall is punctured. Carefully examined, these proved to be unmistakably *Halicystis*, although of uncertain species. The previous ascription of this plant in the floras[3] to *Valonia ventricosa* J. Ag. illustrates its close resemblance in general habit to that single-celled species, also frequently washed ashore on beaches in the West Indies and Florida (Børgesen, 1913; Taylor, 1928). The affinities of the Bermuda flora with that of the latter regions naturally suggested the identity of the plants, especially since no *Halicystis* of this size had been described, and most of its collections were from colder seas. But over seven years of collecting by ourselves and others interested wholly in *Valonia* has turned up no specimen of *V. ventricosa* in Bermuda, and it seems likely that it is absent from the flora. (We are now attempting to introduce it. *V. macrophysa* Kütz., a much branched species, is common.) The only evidence that it may have

[3] Collins, F. S., and A. B. Hervey. Algae of Bermuda. Proc. Am. Acad. Arts and Sci. **53**: 51. 1917. Howe, M. A. in N. L. Britton. Flora of Bermuda 494. New York, 1918.

occurred is Murray's curious statement that he found in his specimens from Bermuda small vegetative cells inside the old cell walls, a form of reproduction very characteristic of *Valonia ventricosa*, but rarely if ever seen in *Halicystis*. Indeed it was earlier noted (Blinks, 1927) that the Bermuda 'sea-bottles,' if carefully gathered and kept alive in the laboratory, often develop the striations and dark plates characteristic of zoosporulation in *Halicystis*. These living cells show many differences from living *Valonia ventricosa*, such as floating in sea water (*Valonia* sinks, due to its denser sap), more resilience to the touch (*Valonia* is hard and firm), and a paler color. Also they bear the characteristic single pedicel and often a bit of the *Lithothamnium* substrate (figs. 1, 2). But as generally found on the beaches, killed and bleached by the sun, and rolled about by the waves, with the protoplasm disintegrated, there remains only the fine, elastic texture of its wall, and a fragment of the pedicel, to distinguish this *Halicystis* from *V. ventricosa*, with its coarser, laminated wall (which can be peeled into layers), and numerous small holdfast cells (for illustrations of which see Børgesen, 1913). In dried herbarium material these differences are even less obvious.

It was only when cells of *Halicystis* were found *in situ* at Bermuda, and not cast up on the beaches, that its specific characters could be ascertained. Colonies of such growing cells were found in 1925 by Mr. M. J. Dorcas, whose photographs of them leave no question as to their identity. The morphology and reproduction were not, however, carefully studied until 1929, when we found at the same locality colonies in much greater number, with cells in quantities sufficient for physiological study and for sap analysis, which has been reported elsewhere (Blinks, 1929; Blinks and Jacques, 1930). Parts of such colonies are shown in figures 9 and 10. They occur just below low tide level in rather shaded cool caves and clefts where the algal vegetation is nearly restricted to *Lithothamnium*. On the crust of this coralline (usually *L. mesomorphum* Fosl.) the *Halicystis* cells grow in colonies up to several hundred. Such crusts were broken loose along with bits of rock and brought to the laboratory, where both *Halicystis* and *Lithothamnium* lived for many months in pans of sea water. During this time sporulation occurred with great regularity at intervals of exactly two weeks, at periods coinciding with the first and third quarters of the moon from April through July, when observation was discontinued. Most, although, not all, of the cells were involved at each period. The process of sporulation corresponded in general with the descriptions of Kuckuck (1907), as Smith also found. There was first a collection of the chloroplasts into radial or slightly spiral striations, converging toward the apex of the cell (fig. 5*a*). In about a day's time there appeared the characteristic

crenate plates of densely crowded chloroplasts. In our material the majority of these were the dark plates, found by Kuckuck to produce the so-called macrozoospores. Typical examples are shown in figures 6 and 7. The clear spots in the center of these plates are slightly protruding papillae, which are the exit pores for the zoospores, formed in great abundance throughout the dark plates. Many of the megazoospores did not escape but remained swimming about in the vacuole for several hours. They then sank to the bottom of the cell into a dark mass which was often reabsorbed into the protoplasm. The chloroplasts also moved back into the region of the previous dark plate, and restored a uniform color to the cell, which usually recovered completely within a day after the formation of spores. In some cases, however, the mass of zoospores obviously injured the basal protoplasm or was even extruded (fig. 8).

The paler, opaque plates noted by Kuckuck were also formed in our material (fig. 5*b*), but in smaller number than the dark plates. Unfortunately they seldom matured, and active microzoospores were but once observed in a cell. These could not be isolated for measurement, but appeared to be about 4μ in diameter. We have therefore not yet been able to verify in our material the fusion of megazoospores with microzoospores as gametes, reported by Smith in the Pacific coast *H. ovalis*. Neither have we observed the expulsion of jets of spore masses through the papillae, as seen in one of Smith's cells. The force for such a discharge is at hand, however, in the turgor of the cells, a fine jet of sap being released when the cell is pricked. If this occurs under water a free cell is sent spinning for several seconds by the force of the stream, the cell shrinking noticeably in size during this time. The wound then heals and the cells recover in a day or two their original size and turgor. This recovery frequently occurred after the extraction of sap for analysis (Blinks and Jacques, 1930). Such healing of punctures must be of benefit to the plants, exposed as they are to wave action, and it undoubtedly accounts for the numbers of cells broken loose, without permanent injury, by the heavy surf of the Bermuda south shore, to continue life for an indefinite period while floating free at the surface.

The attached and stranded cells show no differences other than color and size (the stranded cells being usually paler and larger), but form a graded series (see fig. 3), which persuades us that they are all of the same species. The proposal of the new species, *H. Osterhoutii*, is based upon three characters which distinguish it from *H. ovalis*, the only other well established species. These are:

1. Size. The cells reach a diameter of 3 cm. or more, while the largest recorded cell of *H. ovalis* is 1.5 cm. (Smith).

2. Chloroplasts. These possess pyrenoids, which can be seen with diffi-

culty in the living cell, but are very clear in the protoplasm when mounted on a slide. Pyrenoids are lacking in *H. ovalis*, as described in the literature, and confirmed by our recent examination of Dr. Hazen's specimens from California.

3. Zoospores. The megazoospores are broader and more spherical than in *H. ovalis*. The latter are 7 to 8μ wide and 12 to 14μ long, while those of *H. Osterhoutii* range from 9 to 12μ wide and 10 to 15μ long, but are mostly nearly spherical and 10 to 11μ in diameter.

Megazoospores and chloroplasts of *H. Osterhoutii* are shown in text figure 18.

It should be noticed further that the Pacific *H. ovalis* is described by Smith as having the pores for the escape of zoospores on a 'transverse belt encircling the globular portion of the vegetative cell.' In *H. Osterhoutii* the pores lie much nearer the apex, forming an irregular line on an apical crenate plate or subapical crescent (fig. 7).

Finally, in a physiological character, the high sodium content of the vacuolar sap (Blinks and Jacques, 1930), *H. Osterhoutii* differs markedly from the only other *Halicystis* so far analyzed. This, *H. ovalis* from the Pacific, is reported by Brooks (1930) to have a much greater proportion of potassium chloride. Which, if either, of these saps is characteristic of the genus cannot be stated in the absence of analyses for the European forms.

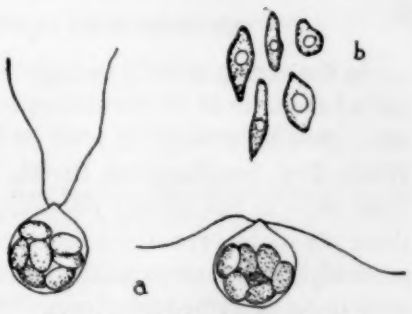


Fig. 18. *Halicystis Osterhoutii*. a, megazoospores; b, chloroplasts, showing pyrenoids. ×1000.

It is possible that future study of the reputed *H. parvula* of the Mediterranean, may show it to be identical with *H. Osterhoutii*. Its occurrence in warm water suggests this, and it is said by Murray to possess pyrenoids in the chloroplasts. We can find, however, no record of any description of the species by Schmitz. The other characters quoted by Murray, such as small size, short blunt stalk, and rough surface, are not in agreement with *H. Osterhoutii*, but may not be important specific differences. Feldmann (1929) questions its inclusion in *Halicystis*, since nothing is known of the structure of its base; it was possibly a specimen of *Valonia*, as Feldmann found to be the case with a former record of *H. ovalis* in the Mediterranean. The presence of pyrenoids in an undoubted *Halicystis* like *H. Osterhoutii*, however, raises the presumption of its correctness, and it is to be hoped that it will again be found and compared in morphology and reproduction with the present species.

Halicystis, possibly identical with the Bermuda form, may apparently be expected in other tropical or subtropical regions. A few small cells, floated in upon the beach at Dry Tortugas, Florida, were found by one of us in 1926 and again in 1929, but a search there yielded no growing cells nor any localities favorable to them. They may have come from some depth, as do probably also the stranded Bermuda cells. Study of specimens in the New York Botanical Garden herbarium indicates that a collection of '*Valonia ventricosa*' from Rose Key, Bahamas, is likewise *Halicystis* (*M. A. Howe 3394*). It probably occurs elsewhere in the West Indies, although the Guadeloupe record of '*Valonia ovalis*' by Mazé and Schramm[4] is apparently due to confusion with *V. ventricosa*, for which the habitat is appropriate. De Toni makes this correction in *Sylloge Algarum* (**1**: 374). A similar correction is made by Børgesen (1913, p. 28) for the old records of *V. ovalis* at St. Croix, Virgin Islands.

CORYNOMORPHA CLAVATA (HARVEY) J. AGARDH

In the spring of 1929 and again in 1930 this interesting and seldom reported member of the Grateloupiaceae was found in considerable abundance, growing at low tide level on the outer sides of 'boiler' reefs off West Whale Bay, Southampton Parish, Bermuda. The difficulty of inspecting these reefs in the usually prevailing surf may account for the absence of these plants in previous collections. They are very firmly attached and probably are not often washed ashore. The plants agree in every respect with those described by Harvey (1853, p. 196) (as *Acrotylus clavatus;* cf. Taylor, 1928, p. 197) from material washed ashore at Key West, Florida. The thallus is up to 6 cm. long and 8 mm. wide, club-shaped, terete, obtuse at the apex, tapering below to a thickened colar, from which it again tapers to a filiform stipe and discoid hapteron. The thallus is simple or branched, dark purplish red in color, often greenish at the tip. In life the plant is firm and crisp but on drying without pressure, as Harvey noted, it shrinks prismatically, persisting in this angularity even when again moistened. Harvey suggested that the species *C. prismatica* is probably based upon such dried specimens. No fertile material was found. This is apparently the first record of the growing plants in America. Figures 13 to 16 give a good idea of the intact plant, and figure 17 of pressed dry specimens.

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[4] Maze, H., and A. Schramm, op. cit. p. 102.

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Description of plates 22, 23

PLATE 22. *Halicystis Osterhoutii*

Fig. 1. Characteristic stranded cell. This is the 'sea-bottle' as washed up on the beaches (×1.5).

Fig. 2. Stranded cells showing pedicel, one with a piece of *Lithothamnium* still attached (×1.5).

Fig. 3. Comparison of sizes of a large growing cell, found attached (left) with 3 smaller stranded cells (×1.5).

Fig. 4. Very young cells in their position of growth on *Lithothamnium* crust (×2.2).

Fig. 5. Beginning of zoosporulation. (*a*) An early stage, with chloroplasts arranged in striae leading toward the apical disc. (*b*) A later stage with pale disc which produces microzoospores (×3).

Fig. 6. Cells showing the crenate dark discs of megasporulation, with clear papillae through which the spores escape (×2).

Fig. 7. Similar stage (×3).

Fig. 8. Cells after zoosporulation. In the cell to the right the zoospores, liberated into the vacuole but not escaped, have fallen to the bottom in a dark mass which has injured the protoplasm, leaving a clear spot near-by. In the cell at the left a protuberance has been formed where the zoospore mass sank to the bottom of the vacuole (×3).

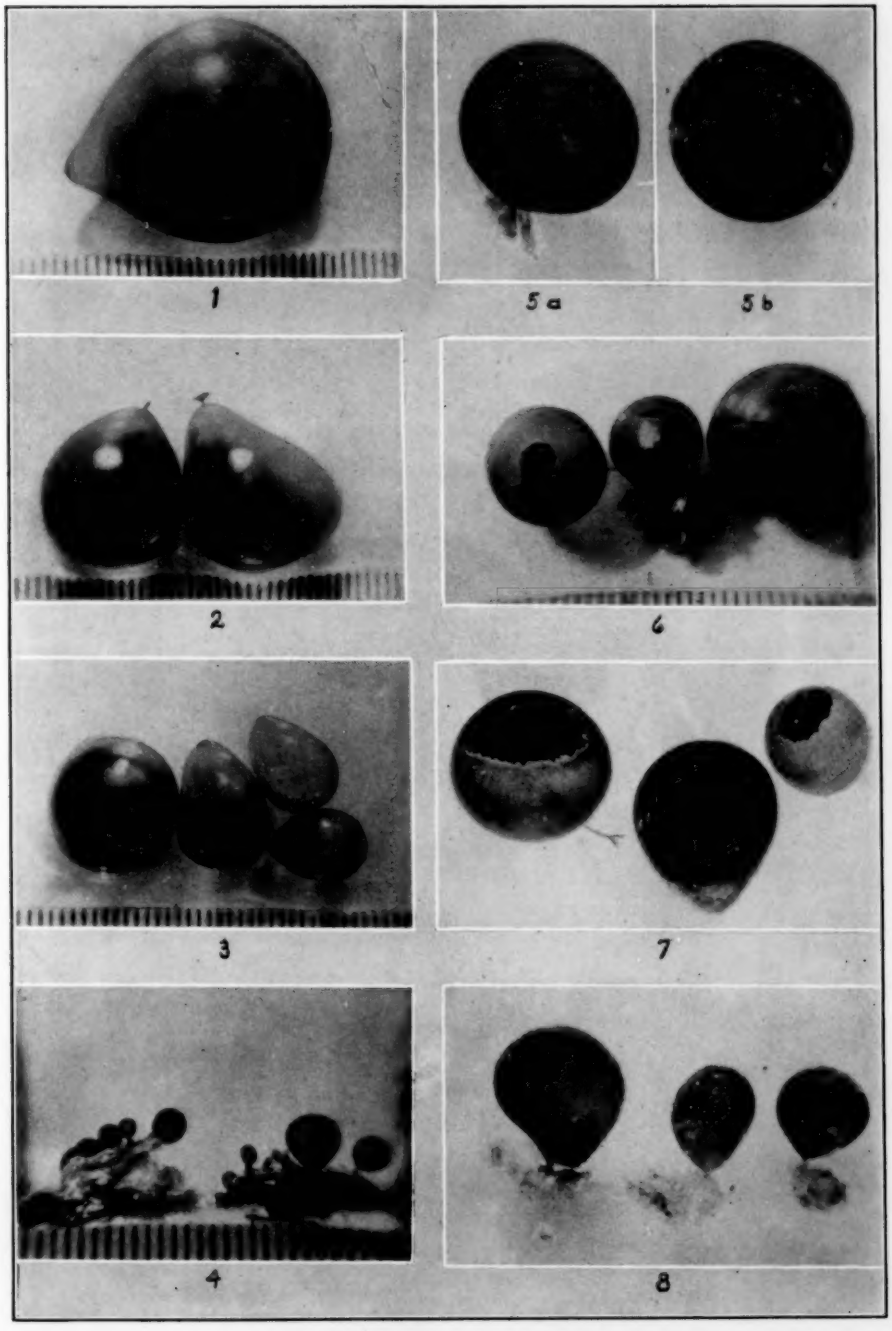
PLATE 23

Figs. 9, 10. Colonies of *Halicystis Osterhoutii* on *Lithothamnium* encrusted rocks (×2). Figure 9 shows some small cells of *Valonia macrophysa* in lower left.

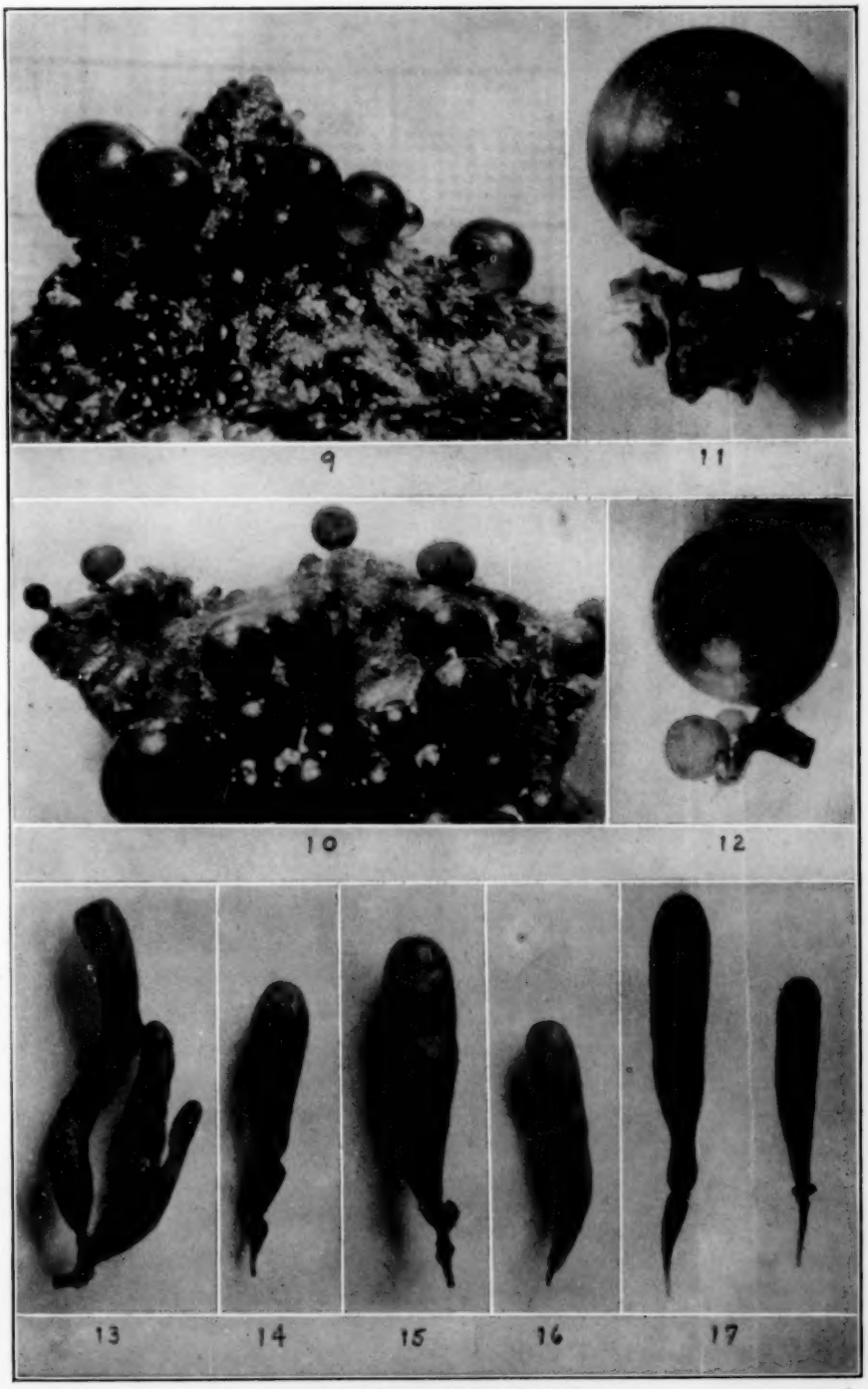
Figs. 11, 12. Detail of cells showing attachment to *Lithothamnium* (×4). In figure 11, *Lithothamnium* has grown partly over the base of the cell.

Figs. 13, 14, 15, 16. Habit of *Corynomorpha clavata* (Harvey) J. Agardh. (×1.2).

Fig. 17. Dried herbarium specimens of *Corynomorpha clavata* (×1.2).



HALICYSTIS OSTERHOUTII BLINKS AND BLINKS



HALICYSTIS AND CORYNOMORPHA

UNIV. OF MICH.

Notes on Fabaceae—XIII

PER AXEL RYDBERG

TIUM Medic[1]

The genus was established in 1787 by Medicus, on two European species, evidently closely related to the first section of North American species treated below. When the writer in 1906 (Bull. Torrey Club **32**: 659) accepted this genus and admitted to it American species, three species of this section were transferred. This first section corresponds to Gray's, Watson's, and Jones' section Galegiformes.[2] Gray and Watson, when they described *Astragalus Howellii* and *A. misellus*, implied that these also belong to the same section. Jones included them and their relatives in his Hamosi. The rest were placed by him in various sections to which they are not related.

1. RACEMOSA

This is equivalent to Gray's section Galegiformes of *Astragalus*.

1. TIUM DRUMMONDII (Dougl.) Rydb. This species is well understood, differing from the rest in the soft loose pubescence and pod cordate in cross-section. It is distributed from Saskatchewan and Alberta to northern New Mexico and Utah. It is rare west of the continental divide.

2. TIUM BREVISETUM (M. E. Jones) Rydb. Jones described his variety *Astragalus racemosus brevisetus* (Proc. Calif. Acad. II. **5**: 262. 1895) from specimens collected by himself at Ramos, Zacatecas, giving as the most distinctive characters that the calyx is spurred and the 'setae at the base line long.' In the type (so marked by Jones) in the United States National Herbarium, the calyx is not spurred. I presume that Jones by the word 'setae' meant the bracts, as he characterized his other variety (*longisetus*) as having 'long hyaline setaceous bracts.' I believe that the Mexican type is distinct from *T. racemosum*, and that the short calyx-teeth and thicker leaflets are better characters than the shorter bracts. The other two specimens, *Carleton 221* from Oklahoma and *Rydberg* from Curtis Creek, Nebraska, are merely specimens of *T. racemosum*. In his *Revision of Astragalus*, Jones does not include Mexico in the range of his var. *brevisetus*, though the type came from there.

[1] The arrangement of sections and numbering of species in this article follows exactly that set forth by the writer in his recent elaboration of the genus *Tium* for the North American Flora (**24**: 384–399. 26 Jl 1929); keys and descriptions are therefore unnecessary here.

[2] It is to be noted that *Astragalus galegiformis* of Europe does not belong to this section.

3. TIUM RACEMOSUM (Pursh) Rydb. *Astragalus racemosus* Pursh was described from specimens collected by Bradbury on the Upper Missouri, probably in South Dakota. Nuttall described *A. galegoides* from the White River, South Dakota. Perhaps the types were collected together. The plant is distributed from North Dakota to Oklahoma, Colorado and eastern Wyoming.

4. TIUM PLATYCARPUM Rydb. The type was collected along Oak Creek, southern Colorado, in 1873, *Brandegee*. For some time, I thought that it might be the suppressed *Astragalus subcompressus;* but Gray's description of the pod shows that the latter must be the same as *A. scopulorum* Porter.

5. TIUM SCOPULORUM (Porter) Rydb. This resembles a good deal *T. racemosum* in habit, but the pod is different, the septum being very broad and nearly reaching to the upper suture. The leaflets as a rule are comparatively broader and shorter. *Astragalus subcompressus* A. Gray and *A. rasus* Sheldon are synonyms. Its range extends over Colorado, New Mexico, and southern Utah.

6. TIUM STENOLOBUM Rydb. Two sheets of this species had remained unnamed for ten years in the herbarium of The New York Botanical Garden. As neither had any fruit, the proper position of the species could not be determined. The specimens of the same number in the National Herbarium, however, have young fruit, and the species evidently is closely related to *T. scopulorum* (Porter) Rydb., differing in the long calyx-teeth and the acute leaflets.

NEW MEXICO: Sandia Mountains on the eastern slope at Palomas, *Charlotte C. Ellis 326* (type).

2. MISELLA

Jones included the species of this group in his Hamosi, which contains a mixture of at least five groups with different types of pods. The largest of these groups I have placed in genus *Hamosa*. The species of this section Misella have pods nearly completely 2-celled, and therefore approach closely the genus *Hamosa*, but the pod is distinctly stipitate and in structure fully agrees with that of the section Racemosa except that the septum is broader. A few species of *Hamosa* have short-stalked pods but the stalk is formed by as light production of the receptacle and not a true stipe, i.e., not an attenuation of the lower portion of the pod itself.

7. TIUM ARTHURII (M. E. Jones) Rydb. resembles *T. Howellii* in habit but the pod is fully half longer and nearly straight. Jones in the original description compared it with *Astragalus Congdoni* and *A. Layneae*, to which it is not related. In his *Revision of Astragalus*, he placed it next *A.*

Traskiae. Some years ago (Bull. Torrey Club **40**: 51. 1913), I erroneously referred this species to *Atelophragma*, not knowing the mature pod. In Heller's specimens in the Columbia University herbarium, the pod is only half-grown, but better material has been furnished by Sheldon from Oregon and Washington.

IDAHO: Lake Waha, *Heller 3259* (type).—WASHINGTON: Grand Ronde, Asotin County, *Sheldon 8218*.—OREGON: Jim Creek, Wallowa County, *Sheldon 8288*.

8. TIUM HOWELLII (A. Gray) Rydb. Gray described this species from Wasco County, Oregon, and placed it in his section Galegiformes, next to *Astragalus Drummondii*, acknowledging its relationship to the genus *Tium*.

OREGON: Southern Oregon, *Howell*, 1879–1880; Dalles, *Howell;* Pendleton, *Mackenzie 1915*.

9. TIUM MISELLUM (S. Wats.) Rydb. In the original publication, this also was placed in the *Galegiformes* by Dr. Watson.

OREGON: Mitchell, Wasco County, *Howell*, in 1885; Grant County, *Cusick 1690;* Crook County, *2632; Leiberg 322;* Wheeler County, *Peck 10101*.—WASHINGTON: Ellensburg, *Piper 2681, Whited 84*.

10. TIUM INYOENSE (Sheldon) Rydb. The nearest relatives of this species are probably *T. Nevinii* and *T. Traskiae*, but the plant is very different in habit, and the texture of the pod is much thinner than in any of the species of *Tium* and more like that of *Atelophragma*, though the shape is that of the two species mentioned. It is known only from the type locality, Darwin Mesa, Inyo County, California.

11. TIUM NEVINII (A. Gray) Rydb. Dr. Gray placed this species also in his section Galegiformes, stating that 'it seems to be a little related' to *Astragalus Drummondii* and *A. racemosus*. On account of the cinereous or white pubescence, this and the next differ from the rest in general appearance. They have also much shorter pods.

CALIFORNIA: San Clemente Island, *Nevin & Lyon; Trask 279;* Santa Barbara Island, *Trask*.

12. TIUM TRASKIAE (Eastw.) Rydb. This is known only from the type locality, San Nicholas Island, and from Santa Barbara Island, both collected by Mrs. Trask.

3. ARRECTA

The pod of this section, especially that of *T. eremiticum* and *T. arrectum*, differs little from the pod of the Racemosa, except in not being pendent. It therefore approaches more the pod of the type species of the genus, *Astragalus sulcatus* of Europe.

This constitutes a part of Jones' section Reventi-Arrecti, which is a great mixture: *Astragalus reventus* having its nearest relatives in Jones' section Ocreati; *A. Cimae* being most closely related to *A. Beckwithii; A. Bolanderi, A. vallaris, A. accidens,* and *A. Hendersoni* forming a group by themselves, the genus *Hesperonix; A. obscurus* and its relatives, which Jones placed in his Atrati, though they are closely related to *A. arrectus,* differing in the very short, almost obsolete stipe. The same can be said of *A. glaber,* which Jones placed in Hamosi, and *A. terminalis* which he included in Uliginosi.

13. TIUM EREMITICUM (Sheldon) Rydb. The type of *Astragalus eremiticus* Sheld. was collected by C. C. Parry at Beaverdam, 'Southwestern Utah' [now Arizona]. It was originally named by Watson *A. arrectus,* but differs from that species in the long stipe and the better developed septum.

The northern form has shorter racemes, with the stipes in fruit more arching, but is scarcely distinct. It was first collected by Watson at Coyote Mountains, Nevada, and mistaken for *A. arrectus.* It was described as *A. eremiticus Spencianus* Jones and later as *A. boiseanus* A. Nels. Jones in his *Revision,* treated it under the name *A. arrectus Kelseyi,* which was a rather poor identification, for *A. Kelseyi* is the same as *A. atropubescens* Coult. & Fish., the two being described probably from different specimens of the same collections. I myself also made a great blunder, when I referred *A. boiseanus* to *Cystium,* thinking that the name *A. boiseanus* belonged to a species which I afterwards published as *C. heliophilum,* and which turned out to be the same as *A. salinus* Howell.

A specimen from Clorida, Arizona, collected by Jones in 1903, looks quite unlike the type, having purplish stems, purple flowers and large pods, but can not be separated specifically. Another similar specimen comes from Peach Springs, *Lemmon,* in 1884. The species has a rather extensive range, extending from Arizona through Utah and Nevada to Idaho and Oregon.

14. TIUM MALHEURENSE (A. Heller) Rydb. *Astragalus malheurensis* A. Heller was based on *A. Cusickii* Rydb., which name was preoccupied. It is closely related to the preceding and perhaps not specifically distinct. The type came from Malheur, Oregon, *Cusick 1238.* It has also been collected at Vale, Malheur Co., *Leiberg 2061,* at least in part, and at Weiser, Idaho, *Jones,* in 1899 and 1900.

15. TIUM ARRECTUM (A. Gray) Rydb. The type of *Astragalus arrectus* was collected on the Kooskooski River (now Clearwater), by Geyer. Jones gives as synonyms of this species: *A. leucophyllus* Hook., *A. atropubescens* Coult. & Fish., *A. palousensis* Piper, *A. Cusickii* Rydb., and *A. malheur-*

ensis A. Heller. *A. leucophyllus* Hook. is a synonym, and so is probably also *A. palousensis* Piper, but the rest do not belong to it. *A. atropubescens* has a glabrous pod, with a well developed partial septum, while in *A. arrectus* the pod is strigose and the septum almost obsolete. *A. Cusickii*, of which *A. malheurensis* is a substitute, has a more elongate stipe and well developed septum. See notes on the preceding species.

IDAHO: Moscow, *Abrams*, in 1900; Salmon, *Payson & Payson 1882.*—WASHINGTON: Pullman, *Piper*, in 1901; *Jones*, in 1905; *Williamson; Hardwick*, in 1895; *Elmer 288; Piper 1493;* Spokane River, *Wilkes Expedition.*—OREGON: Wallowa County, *Sheldon 8095.*—MONTANA: Anaconda, *Jones*, in 1905.

16. TIUM REMOTUM (M. E. Jones) Rydb. This is characterized by being suffruticose below and by its long and lax racemes and smaller, strongly ascending flowers. It is known only from the type locality, Good Springs, Nevada. Some of the duplicates have been distributed erroneously under the name *Astragalus Pattersonii.*

17. TIUM ATROPUBESCENS (Coult. & Fish.) Rydb. The type of this species was collected at Deer Lodge, Montana, by Kelsey, July 9, 1892; that of *Astragalus Kelseyi* at the same place, by the same collector and on the same date; probably the two represent specimens from the same collection. The plant is more pubescent than is *T. arrectum;* the pod is glabrous and with a well developed partial septum.

MONTANA: Deer Lodge, and Helena, *Kelsey;* Beaverhead County, *Tweedy 8;* without locality, *F. W. Anderson;* Anaconda, *Blankinship 114.*—IDAHO: Lehmy Forest, *Eggleston 13988.*

18. TIUM LEIBERGII (M. E. Jones) Rydb. This is closely related to *T. arrectum* but differs in the pod, which is sparingly black-strigulose and has a better developed septum; the leaves are gathered near the base of the plant and the leaflets are linear.

WASHINGTON: Egbert Springs, *Sandberg & Leiberg* 354 (type).[8]—IDAHO: *Payson & Payson 1882;* Custer Co., *Macbride & Payson 3332;* Moscow, *Henderson 2744.*

19. TIUM MICHAUXII (Kuntze) Rydb. As *Astragalus glaber* Michx. was not tenable, Sheldon proposed the name *A. apilosus.* The reason why he did not adopt Kuntze's specific name (*Tragacantha Michauxii*), was that there was already an *Astragalus Michauxianus* Boiss. Following Sheldon, I made the error of using the specific name *apilosum* when transferring it to *Tium*, in which genus Kuntze's specific name is perfectly legal. Gray placed the species in his section Austro-occidentales, a very unnatural group. Jones in his monograph placed it in the section Hamosi, where I

[8] Some of the duplicates bear the number 359 and are labeled *Delphinium simplex.*

do not think it belongs, its pod being not completely 2-celled and short-stipitate. Not withstanding the taller habit, its relation is with *A. obscurus* and *A. arrectus*.

NORTH CAROLINA: Cumberland County, *Curtis;* Bladen County, *Biltmore Herbarium 1541 a; Ashe,* in 1898.—SOUTH CAROLINA: Aiken, *Canby,* in 1869; *Ravenel;* Hertville, *Coker,* in 1909.—GEORGIA: Bulloch County, *R. M. Harper 914, 907;* Augusta, *Cuthbert 194;* Reed.—FLORIDA: *Chapman 147.*

20. TIUM TERMINALE (S. Wats.) Rydb. Watson describes this species as having purplish flowers and being related to *Astragalus adsurgens*, which evidently led both Jones and myself astray. I admitted it in my *Flora of the Rocky Mountains* as a species of *Astragalus*, and Jones in his *Revision* still regarded it as a species of *Astragalus* proper, though he transferred it to the section Uliginosi. The pod of the species, however, is almost exactly that of *A. obscurus*. Furthermore the flowers on the type sheet in the Gray Herbarium, though faded, show no trace of purple, except on the tip of the keel. Shear's specimens and my own had ochroleucous flowers with purple-tipped keel. Jones described his *A. reventoides* and compared it with *A. reventus*. According to the original description, the pod should be oblong-oval. I had not seen Jones' type but judging from the description I thought it must be related to *A. reventus* and hence a *Cnemidophacos*. Jones has discovered the relationship between *A. terminalis* and *A. reventoides*, making the latter a variety of the former, adding the remark: 'A poor variety.' I think they are identical. Jones (Contr. **10:** 68. 1902) erroneously stated that *A. Kelseyi* is the same. This error he admits later (Contr. **12:** 11. 1908), but refers it (again erroneously) to *A. arrectus*, 'a form approaching the variety *Spencianus*' (see my notes under *Tium eremiticum*).

MONTANA: Red Rock Creek, *Watson 87* (fl. & fr.); Lima, *Shear 3383* (fl.); *Rydberg 2703* (fl.).—IDAHO: *Henderson 3731.*—WYOMING: Teton Forest, *Morris 266.*

21. TIUM OXYTROPOIDES (M. E. Jones) Rydb. This is closely related to *T. conjunctum*, and Jones in his *Revision* included it in *Astragalus reventus conjunctus*, but the calyx is white-hairy, instead of black-hairy, the pod is also white-strigose, and the leaflets very narrow. The stems proper are very short and the height of the plant is mostly made up by the long peduncles.

OREGON: The Dalles, *Howell 798;* Wasco Co., 12 miles southeast of The Dalles, *Lawrence 99* and *116.*

22. TIUM SHELDONI Rydb. It is related to *T. obscurum* and *T. conjunctum*, having the same pod, but differing from the former in the stems

being upright, the peduncles longer, the leaflets longer and narrower, and the flowers larger. It differs from the latter in the pubescent pod, the loose pubescence of the leaflets, and the calyx, which is less conspicuously black-hairy. It resembles *T. Leibergii* more in habit, but in that species the stipe is about as long as the calyx-tube.

OREGON: Horse Creek Canyon, Wallowa County, May 14, 1897, *Sheldon 8032* (herb. N. Y. Bot. Gard.); *8345; 8095.*

23. TIUM CONJUNCTUM (S. Wats.) Rydb. *Astragalus conjunctus* S. Wats. was described from specimens collected by Joseph Howell in John Day Valley in 1880. Jones (Contr. W. Bot. **10**: 61. 1902) made it a variety of *A. reventus* without any remarks. In his *Revision* he describes the pod as 'distinctly inflated,' while Watson had described it as 'narrowly oblong.' In fact, the pod resembles much that of *T. arrectum*, except that it is sessile or nearly so as in *T. obscurum*. The plant resembles *T. reventum* in habit only, and so does *T. arrectum*, but both the corolla and the pod are different. Jones furthermore gives *A. Hoodianus* Howell and *A. conjunctus oxytropoides* Jones as synonyms. *A. Hoodianus* is related to *A. reventus*, having the 'inflated pod.'

OREGON: Malheur County, *Cusick 2374;* Morrow County, *Leiberg 73;* Anderson Valley, *2391;* Mitchell, *T. Howell*, in 1885; Grant County, *Cusick 2805;* Wasco County, *Peck 10022;* Blue Mountains, *Lawrence 864;*—WASHINGTON: Asotin County, *Sheldon 8236;* Ellensburg, *Canby 724;* Harney, *Coville 594.*

24. TIUM OBSCURUM (S. Wats.) Rydb. This is characterized by the stems decumbent at the base, the short and broad leaflets, and the ochroleucous flowers less than 1 cm. long.

NEVADA: Truckee Pass, *Watson 260;* Empire City, *Jones;* Reno, *Jones 3842; Heller 9582;* Eagle Valley, *Stretch*, in 1865; Virginia City, *Jones 9;* Washoe County, *Sonne 7;* Great Desert, *Lemmon;* Panaca, *Coville & Funston 1975.*—CALIFORNIA: *Lemmon 62.*

25. TIUM MISERUM (Dougl.) Rydb. *Astragalus miser* Dougl. was described in a footnote and the diagnosis is altogether inadequate. Dr. Gray thought that he had identified the plant with *Lyall 7*, collected in flower only. The latter specimen belongs to *Phaca microcystis* A. Gray, or a closely related species. Following Gray, Piper (Contr. U. S. Nat. Herb. **11**: 373. 1906) adopted the name *Phaca misera* for *Astragalus microcystis*. The director of the British Museum has kindly sent us a photograph of Douglas' specimen of *A. miser* found in their collection. This photograph shows a plant in bud and young flowers, wholly unlike *A. microcystis*. The only species of North Western United States that resembles the photograph in habit is one, which I regarded as an undescribed one and related to *A.*

obscurus S. Wats. Although I have not seen any specimen of this from Spokane River, the type locality of *A. miser*, I think that it is the same. It is closely related to *T. obscurum*, but is a more tufted plant, with shorter, erect or ascending stems and narrow leaflets. *Leiberg 2033* was originally labelled *A. misellus*, to which it is not closely related. Most of the other specimens have been distributed as *A. obscurus*.

OREGON: Baker County, *Cusick 2368; 392;* Malheur County, *Leiberg 2033, 2292;* Burns, *Peck 3018;* Lake County, *Eggleston 6872, 6767.*—IDAHO: Dixie, Elmore County, *Macbride & Payson 2851.*—NEVADA: Jarbridge, *Nelson & Macbride 1984.*—CALIFORNIA: Goose Lake Valley, *Austin & Bruce 2211* (mainly); *2215* (in part); Modoc Co., Lemmon, in 1899; *Mrs. Austin*, in 1894.—WASHINGTON: Yakima Region, *Tweedy 601.*

4. ATRATA

As the pod is almost completely 2-celled, the writer some years ago thought that *Astragalus atratus* S. Wats. belonged to the genus *Hamosa*, and described a closely related species as *Hamosa atratiformis*. The pod in *A. atratus* is however stipitate and the septum does not fully extend to the upper suture, and besides its flowers and general habit resembles much *T. obscurum* and still more a related species, *T. miserum*, treated above. On the other hand, the closely related species *T. owyheense* has hardly any septum. It has seemed best to include these species in *Tium* and forming a section by themselves and differing from the Arrecti in the reflexed pod.

26. TIUM ATRATUM (S. Wats.) Rydb. This species was described from specimens collected from Pah-Ute and Toyabe Mountains, Nevada, *Watson 265*. Those of the same number from Havallah Mountains cannot be determined as they are in flowers only. Jones redescribed the typical form as var. *stenophyllus*. Noticing his error, he proposed the varietal name *phyllophorus* for what he had regarded as the typical *A. atratus*. As the writer has not seen the type of the latter, he cannot tell whether this is distinct enough.

NEVADA: *Watson 265* (type); Palisades *Jones 3840, 3841* (with broader and shorter leaflets); *Cusick 422;* Austin, *Hitchcock 669;* Palisades, *Stokes*, in 1903; Toyabe Range near Austin, *Kennedy 4399.*

27. TIUM MENSARUM (M. E. Jones) Rydb. It differs from *T. atratum* in the purple-tipped corollas, the broader leaflets, the broader and more compressed pod, tapering at the base. It is known only from the type locality on Darwin Mesa, Inyo County, California, *Coville & Funston 792.*

28. TIUM ATRATIFORME Rydb. Jones has reduced this to a synonym of his *Astragalus straturensis*, but the resemblance is only superficial, neither the flowers nor the fruit are the same. Tidestrom, misled by Jones' statement, applied the name *A. straturensis* to this species.

UTAH: Washington County, *Parry 47*.—ARIZONA: *Palmer 107*.

29. TIUM OWYHEENSE (A. Nels.) Rydb. As this species resembles *T. atratum* much in general habit, Jones reduced it to a variety of that species, but the pod is quite different, the valves being thinner and mottled, the sulcus on the lower suture being more open and the septum nearly obsolete.

IDAHO: Hot Hole, Owyhee County, *Nelson & Macbride 1881* (type); Weiser, *Jones 6342*.—OREGON: Baker, *Eggleston 12597; Cusick 422; Jones*, in 1902.

30. TIUM SALMONIS (M. E. Jones) Rydb. This is probably most closely related to *T. atratum*, but differs in the broad pod and low habit. Jones compared it with *Astragalus obscurus* and *A. panamintensis*. It differs from the former principally in its broader, mottled and divergent or reflexed pod, and from the latter in the narrow septum of the pod and the short leaflets.

OREGON: Trout Creek, *Howell*, in 1885; Malheur County, *Leiberg 2273* (with very broad pod); Baker City, *Jones*, in 1902; Blue Mountains, *Howell 377;* Union County, *Cusick 38*.

31. TIUM PANAMINTENSE (Sheldon) Rydb. In general habit, it resembles some species of *Homalobus*, as for instance *H. tenuifolius*, but the pod is broader, sulcate on the lower suture, and with an almost perfect septum. It is known only from the type locality, Panamint Mountains, Inyo County, California, *Coville & Funston 606*.

32. TIUM EGGLESTONII Rydb. This species resembles *Atelophragma Rusbyi* in habit, but the corolla is different; the pod is glabrous, stipitate, and of a different structure.

NEW MEXICO: Datil Forest, Socorra County, *Eggleston 17216* (type); Apache County, *17028, 17105, 7042a;* Luna, Catron County, *20232*.

33. TIUM RECURVUM (Greene) Rydb. This species is characterized by its falcate pod, in which the upper suture is more curved than the lower.

ARIZONA: Mountains of northern Arizona, *Rusby* in 1883 (type); Mormon Lake, *MacDougal 72*.

5. ORCUTTIANA

This section contains only one species.

34. TIUM ORCUTTIANUM (S. Wats.) Rydb. Jones placed this species in his section Hamosi, between *Astragalus tricarinatus* and *A. drepanolobus*, but it is evidently more related to *T. Howellii* and *T. misellum*, and neither of these should be included in *Hamosa*, but are more related to *T. racemosum* and its allies.

LOWER CALIFORNIA: Cantilles Cañon, *Orcutt 937;* San Enrique, *Brandegee*, in 1889.

6. PALANTIA

This group contains species which resemble some species of the sections Lentiginosa and Diphysa of the genus *Cystium*, but the pod is firm, coriaceous, elongate and scarcely inflated and the partition does not meet the upper suture and does not reach the tip of the pod. They differ from the species of *Astragalus*, section Uliginosi, in the pod, which tapers more gradually at each end and is membranous in texture, with a partial septum.

35. TIUM PALANS (M.E. Jones) Rydb. The type came from Montezuma Cañon, Utah. Jones made this a variety of *Astragalus Tentiginosus* and made *A. araneosus* a synonym thereof. The latter is a true *Cystium*, though the pod is less inflated than in *C. lentiginosum* and *C. diffusum*. The following specimens belong to *T. palans*.

UTAH: Montezuma Cañon, *Eastwood;* Bluffs, *Rydberg & Garnett 9914;* Rockville, *Jones 5218;* Verken City *5215 e;* Silver Reef, *5163 j.*

36. TIUM AMPLEXUM (Payson) Rydb. It is closely related to *T. palans* and Jones regarded it as a synonym thereof. It is, however, not quite the same, as the pod is decidedly hairy and so also the stem. When preparing my *Flora of the Rocky Mountains*, I had not seen this species, and from the description I thought that it should be referred to *Hamosa*. It is known only from the type locality, Naturita, western Colorado.

37. TIUM WILSONI (Greene) Rydb. This is most closely related to *T. palans*, differing in the white corolla, straight and ascending pod, and white-hairy calyx. Thornber has regarded this as a new species, with *Rose 12108* as the type. His manuscript name is, however, preoccupied. From the description, this species seems to be the same as *Astragalus Wilsoni* Greene.

ARIZONA: Flagstaff, *MacDougal 96* and *140; Rose 12108;* Oak Creek; *Rusby*, in 1883.

38. TIUM URSINUM (A. Gray) Rydb. Jones regarded this as a synonym of *Astragalus mokiacensis*, probably because Gray had labelled *Lemmon 3116* and *3326* as *A. ursinus*, while they both belong to *A. mokiacensis*. The type, collected by Palmer in Bear Valley, south central Utah, shows that it is well distinct, the corolla being much smaller, the banner narrower, the stem more slender and flexuose, the pod strongly ascending, smaller, firmer. Jones (Proc. Calif. Acad. II. **5:** 657. 1895) described under this name something else as the description does not fit the original one. It is known only from the type collection, Bear Valley, Utah.

39. TIUM MOKIACENSE (A. Gray) Rydb. The type of this species was collected at Mokiak Pass by E. Palmer in flowers only. Gray placed it

'next to *Astragalus iodanthus*,' to which it has no relationship. Jones made it a variety of *A. lentiginosus*, but it is not closely related to it. It is true that it has a general external similarity to some of the species of *Cystium*, as for instance *C. araneosum*, but the pod is subcylindraceous, neither papery nor inflated, and the septum incomplete. The relationship is with *T. palans*, differing in the almost straight, pubescent, and ascending pod, the broader obovate leaflets, and the more hairy, when young cinereous, stem.

ARIZONA: Mokiak Pass, *Palmer 105;* Grand Canyon, *Lemmon 3116;* Peach Spring, *3326.*—NEVADA: Mica Springs, *Jones 5058* (?).

THE NEW YORK BOTANICAL GARDEN

INDEX TO AMERICAN BOTANICAL LITERATURE
1921–1930

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the work America being used in the broadest sense.

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